MOVEMENTS AND CONSERVATION OF CUTTHROAT TROUT

by

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ABSTRACT

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Adequate space is crucial to the long-term persistence of cutthroat trout populations, but little information exists about movements, interactions with exotic species, or space requirements. My research goals were to determine the range and duration of movements of cutthroat trout in relation to the time of year, habitat, and the non-native brook trout so that minimum space requirements could be estimated. Radio-tagged cutthroat trout exhibited restricted movements during autumn and winter, but moved sporadically during spring and summer. Of the 26 PIT (passive integrative transponder) tag recaptures one year after marking and releasing 200 fish, 13 had not moved greater than 100 m while the remaining 13 moved a median distance of 797 m. Growth rates did not differ between mobile and sedentary fish nor among reach types. The results indicate that neither mobility nor stationarity is superior to the other, but they are alternative strategies to deal with the unpredictability of stream environments.

When cutthroat trout established residence first, the addition of brook trout as competitors had less effect in displacing the established residents than equivalent densities of cutthroat. This threshold density did not differ between reach types. When the residents were removed and then reintroduced into sections already containing competitors, the residents successfully reestablished in only 20% of trials. Neither reach type, species of competitor, nor size of the resident influenced reinvasion success. Brook and cutthroat trout in allopatry used similar stream positions, but demonstrated mutual displacement when sympatric. Comparison of habitats used indicated that brook trout caused niche shifts in cutthroat trout when sympatric. Based on my data, the majority of isolated populations do not have adequate space for long-term persistence. Results of an analytical minimum stream length model indicate that over 4 km of stream was required to maintain an ending population size of 500 individuals at 40% survivorship with high fish densities and 20 km for low fish densities. Stream length required for 30% survivorship with N = 1000 was approximately 11 km for a population with high fish densities and over 54 km for low fish densities. I propose a restoration initiative incorporating reserve design, stream connectivity, and biotic interactions.

(146 pages)

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PREFACE

Chapter 2, Movements and Growth of Stream-Resident Cutthroat Trout, will be submitted to the Canadian Journal of Fisheries and Aquatic Sciences with my major professor, Jeffrey L. Kershner, as a coauthor. Chapter 3, Interactions Between Non-native Brook Trout and Bonneville Cutthroat Trout: Evidence for Competition?, will be submitted to Ecology with my major professor, Jeffrey L. Kershner, as a coauthor. Chapter 4, Critical Needs for Cutthroat Trout Recovery and Persistence, will be submitted to Conservation Biology with my major professor, Jeffrey L. Kershner, as a coauthor.

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CHAPTER 1

INTRODUCTION

The distribution and abundance of interior stocks of cutthroat trout (*Oncorhynchus clarki*) are in a state of drastic decline. Only 2 of the 13 distinct subspecies of interior cutthroat stocks currently remain stable or increasing in number while the remainder have experienced "catastrophic declines" (Behnke 1992). Bonneville cutthroat trout (*O. clarki utah*;) is the only subspecies endemic to the ancient Lake Bonneville Basin of Utah, and was once well distributed throughout the basin (Behnke 1992). It was believed extinct by the early 1950's (Cope 1955), but some populations still remain. Numerous reasons exist for this decline, but the predominant factors include habitat destruction and fragmentation through various anthropogenic actions (Keller and Burnham 1982; Platts and Nelson 1985; Young 1995), hybridization with introduced rainbow trout (*O. mykiss*) and other subspecies of cutthroat trout (Allendorf and Leary 1988; Behnke 1992), competition with non-native salmonids (Hearn 1987; Fausch 1988; Krueger and May 1991), and over-harvest.

Prior to anthropogenic disturbances, trout probably moved freely within and among drainages, exchanging individuals among populations. A highly mobile fluvial component of populations probably used feeder tributaries for spawning and used the main stems of rivers for the remainder of the year, while a less mobile stream-resident component probably lived in the smaller tributaries year round. These two life history

components probably exchanged individuals with every generation, compensating for and hedging against losses due to disturbances (drought, fire, floods, etc.).

Open connections between drainages and the potential for frequent dispersal between populations probably resulted in a metapopulation structure—a group of discrete populations linked by dispersal (Levins 1969). Metapopulations may be important for maintaining salmonid populations with moderate rates of dispersal (Rieman and McIntyre 1993), and theoretically make some species resistant to disturbance (Stacey and Taper 1992; Hanski and Kuussaari 1995) by enabling migrants from one population to refound or maintain another. Island biogeography theory (MacArthur and Wilson 1967) predicts inverse relationships for the distance between patches or populations and the immigration rate between them, and for patch size and extinction rate. Therefore, those populations inhabiting small areas and/or located far away from other populations are at a greater risk of permanent extinction (as opposed to being refounded).

Despite risks incurred with small population sizes or large distances from other populations, even small amounts of migration can rescue populations from extinction (Brown and Kodric-Brown 1977). Increasing dispersal between populations should increase persistence time of populations (Hanski 1991). Using a stochastic simulation model based on demographic parameters collected in the field for the acorn woodpecker, *Melanerpes formicivorus*, Stacey and Taper (1992) reported a short time to extinction in a closed population. Conversely, incorporating immigration into the same model increased population persistence to more than 1000 years. Beier (1993) reported that even low rates

of immigration substantially increased the time to extinction in a cougar population living in a habitat fragment.

Metapopulation theory typically assumes multiple landscape pathways between populations (Levins 1969; Gilpin 1990) because, in terrestrial systems where these concepts were developed, dispersal across the landscape is two-dimensional when viewed in Cartesian space. Streams move across two-dimensional space, but an organism moving within this space is constrained to a one-dimensional pathway. Any barriers encountered will stop upstream dispersal and potentially limit downstream dispersal, whereas in terrestrial landscapes there is often the potential to go around a barrier. An additional problem is that the closer two populations are in space, the greater the degree of correlation in their population dynamics (Hanski 1991). This can dramatically shorten the lifetime of a metapopulation (Gilpin 1990). Also, aquatic systems are longitudinally linked so that actions upstream influence downstream areas (Vannote et al. 1980). Because of this and the one-dimensional nature of streams, correlated environments could set up a negative feedback cycle with low dispersal in populations during years of low abundance. Years of high abundance could result in poor survival of dispersers due to lack of space and density-dependent effects.

The problems imposed on organisms moving through streams become accentuated as natural and anthropogenic disturbances fragment habitats. Fragmentation is the process and result of subdividing contiguous areas or habitats into smaller areas separated by non-useable or marginal areas. The risk of extinction increases as habitats become

fragmented, especially as the degree of isolation from other populations increases (Fritz 1979; Smith 1980; Hanski 1986; Sjogren 1991). Fragmentation results in the loss of habitat, producing discontinuities in historical ranges and creating movement barriers that inhibit the exchange of individuals between populations.

Most subspecies of cutthroat trout currently exist in only small portions of their historical range. Westslope cutthroat trout (*O. c. lewisi*) exist in only 11% of their historical range in Idaho and only 27% in Montana (McIntyre and Rieman 1995), while Colorado River cutthroat trout (*O. c. pleuriticus)* currently inhabit only 1% of their historic range (Behnke 1979). The same trend exists for almost all of the various subspecies, including the Bonneville cutthroat trout, which currently occupies only 5% of its native range (Kershner 1995).

Numerous anthropogenic actions intentionally or unintentionally fragment salmonid habitats. Logging, livestock grazing and agriculture, mining, water diversion for irrigation, and development produce stream conditions unsuitable for salmonids (Meehan 1991). These actions often increase the level of fine sediments in streams, increase water temperature, reduce water quality, dewater channels, or destroy instream habitats. The result is discontinuous fragments that may be isolated from other populations or are too small to maintain self-sustaining populations. Additionally, biotic barriers may be established through interspecific competition, predation, and hybrid zones caused by stocking non-native salmonids. Natural and human-made fish barriers have been used to alleviate the risks of hybridization and competition and restore cutthroat trout

populations. Upstream sections are isolated and undesirable species removed, leaving only native cutthroat trout. This method has had varying success because some barriers are not barriers at all, and people may restock a "restored" section with the undesirable non-natives. If functioning properly, these barriers impede or eliminate upstream dispersal of individuals and further fragment streams and populations.

Many extant cutthroat trout populations are isolated and restricted to headwater reaches of streams with no connections to other populations. As population size and/or amount of habitat declines, stochastic extinction risk increases (Rieman and McIntyre 1993). Small, isolated brook trout (*Salvelinus fontinalis*) populations in Appalachian streams had less than a 50% chance of persisting 30 years according to simulations performed by Nagel (1991). Often the processes causing fragmentation and isolation also degrade habitat quality (fine grained fragmentation) within localized areas and decrease reproductive output or survival. This internal degradation could compound the external effects of isolation and result in a deterministic downslide to extinction. The long-term prognosis for population isolates of cutthroat trout does not look good.

Four main factors probably influence extinction risk for cutthroat trout: total area of available stream habitat, stream habitat complexity, population age structure, and the presence of exotic species. All of these factors acting alone or in concert affect the total length of stream needed to maintain long-term population persistence. It is conceivable that many stretches of stream with all the necessary variables to support an individual may not support a population given current levels of fragmentation. Patch size was

directly correlated with the probability of occurrence of bull trout (*Salvelinus confluentus*), supporting the hypothesis of available area influencing population occurrence (Rieman and McIntyre 1995). Additionally, the strongest remaining populations of many trout species occur in wilderness and roadless areas protected from human disturbance (Gresswell 1995; Kershner et al. 1997).

Population age/stage structure influences the population growth rate and therefore the probability of extinction (Lande and Orzack 1988). All things equal, populations with few reproductively mature individuals will produce fewer progeny than those with more breeding adults. Additionally, missing or underrepresented age classes may indicate habitat deficiencies or other factors limiting population growth and survival.

Complexity of habitat is usually defined in terms of the diversity or abundance of habitat types and structural elements such as logs, rocks, or overhead cover that fish can use as cover (Bisson et al. 1987; Sullivan et al. 1987; Pearsons et al. 1992; Reeves et al. 1993). Increased complexity can provide habitat and refugia from disturbance (Sedell et al. 1990), reduce predation risk (McMahon and Hartman 1989), increase population stability and community resistance to disturbance (Pearsons et al. 1992), and increase species diversity (Reeves et al. 1993). Increased complexity often results in greater abundances of trout and salmon (Lewis 1969; House and Boehne 1985, 1986; Wesche et al. 1987; Moore and Gregory 1988; McMahon and Hartman 1989).

Chapman (1966) hypothesized that food and space regulated salmonid population density because most stream-dwelling salmonids establish territories (Dill et al. 1981;

McNicol and Noakes 1981; McNicol et al. 1985; Grant et al. 1989; Grant 1990; Grant

and Kramer 1990; Keeley and Grant 1995). Increasing food supply can decrease

aggressiveness or the area of territory defended (Symons 1971; Slaney and Northcote

1974) and allow higher densities. Similarly, an increase in habitat complexity or habitat

per unit area can also increase population densities (Hunt 1969; Riley and Fausch 1995).

These factors probably have an inverse relationship with area required for a population;

less food or simplified habitats should require more stream to maintain a given population

size.

The presence of exotic species (especially brook trout) has been proposed to

negatively impact cutthroat trout populations, but the mechanisms and direct effects of

competition are hard to prove conclusively (Hearn 1987; Fausch 1988). However, the

decline in cutthroat abundance coupled with increases in brook trout abundance in

streams provides strong inferential evidence of exotic species negatively impacting

cutthroat trout. Competition for food (exploitation) would probably result in a 1:1

replacement ratio for individuals of equal size. Interference competition could displace

several cutthroat trout for every invading brook trout and require substantially more space

to maintain a cutthroat population with every invading brook trout.

Managers are currently faced with preserving the remnants of interior cutthroat trout

populations despite a lack of information on some basic life history traits. At the most

basic level, trout require sufficient food and shelter to survive. General information is

available on diets (Wilzbach 1985; Bozek et al. 1994) and various aspects of age-specific

habitat use\requirements (Heggenes 1988; Heggenes et al. 1991; Griffith and Smith 1993; Brown and Mackay 1995), but our knowledge breaks down when projected across space and time or when applied to populations instead of individuals. This is largely because generalities underlying the characteristics of both small and large scale trout movements and their relationship to area of stream needed are poorly understood.

The current research was aimed at gaining better insights into cutthroat trout ecology and conservation. My objectives in Chapter 2 were to determine the magnitude, timing, and duration of movements of a stream-resident population of cutthroat trout and to examine potential evolutionary consequences. Chapter 3 investigates the potential for competitive interactions between cutthroat trout and the non-native brook trout. Chapter 4 explores the relationships between population size and space requirements, evaluates current cutthroat trout management strategies, and proposes a conservation and restoration initiative. I conclude with a brief summary of findings and thoughts.

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CHAPTER 2

MOVEMENTS AND GROWTH OF STREAM-RESIDENT

CUTTHROAT TROUT[1]

Abstract: Cutthroat trout (*Oncorhynchus clarki*) implanted with radio transmitters

exhibited a wide range of movement patterns during a 1-year tracking period in an Idaho

stream. Fish moved little during autumn and winter (median = 0 m), more frequently

during spring (median = 576 m), and were variable and sporadic during summer (median

= 425 m). Fish movement through two-way traps was greatest in July and early August

and had stopped almost entirely after early September. Movement timing and frequency

was similar between the traps and the radio-tagged fish. We tagged trout with passive

integrative transponder (PIT) tags, and weighed, measured, and released 167 cutthroat

trout of all size classes throughout a 6 km reach during summer 1995. Of the 26 tag

returns captured 1 year later over 12 km of stream, 13 had not moved greater than 100 m

while the remaining 13 were recaptured at varying distances (median = 797 m). There

were no significant differences in growth rates between mobile and sedentary fish, nor

any growth differences between the high gradient, low gradient, and beaver pond habitat

reach types. Proportions of mobile and stationary fish were not different among the

habitat reach types. The distribution of distance moved was non-random with more

individuals than expected on both the sedentary and mobile tails of the distribution. Our

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[1]Coauthored by Robert H. Hilderbrand and Jeffrey L. Kershner

results indicate that neither mobility nor stationarity is superior to the other, but they are

alternative strategies at either end of a continuum of behaviors to deal with the

unpredictability of stream environments.

Introduction

Much debate and uncertainty exists concerning the movements of stream-resident

salmonids. Until a few years ago, scientists regarded trout as sedentary following

Gerking's (1959) idea of restricted movement in stream fishes, termed the restricted

movement paradigm (RMP) by Gowan et al. (1994). Heggenes et al. (1991) reported

almost 50% of cutthroat trout (*Oncorhynchus clarki*) in their study reach moved less than

3 m from the original point of capture between spring and fall, and only about 18%

moved more than 50 m. Similar results have been reported for brook (*Salvelinus*

fontinalis; Shetter 1968), brown (*Salmo trutta*; Stefanich 1952; Shetter 1968; Bachman

1984; Heggenes 1988), and cutthroat trout (Fleener 1951; Miller 1957).

Evidence also exists for wide ranging movements of trout. A large percentage of

marked cutthroat and rainbow trout (*Oncorhynchus mykiss*) and Dolly Varden (*Salvelinus*

malma) in the Salmon River, Idaho, moved 8+ km over a several month period (Bjornn

and Mallet 1964); many moved 42 km or more. Bernard and Israelsen (1982) and Young

(1996) reported substantial inter- and intrastream movements of cutthroat trout in their

study streams. Similar results have also been reported for brook (Riley et al. 1992;

Gowan and Fausch 1996a,b), brown (Clapp et al. 1990; Meyers et al. 1992; Young 1994)

and rainbow trout (Young et al. 1997a).

Accumulating evidence on trout mobility sparked a reexamination and challenge of the RMP by Gowan et al. (1994), who called for a revision of current views. The data in the studies used to support or refute RMP are often similar, but are interpreted in different ways. The majority of individuals typically remain near the point of capture whereas a variable proportion ($> 20\%$) disperses. To say that salmonids are mobile or sedentary is insufficient because individuals can switch behaviors (Harcup et al. 1984; Brown and Mackay 1995) and may be influenced by the presence of barriers (Young 1996). The identification and understanding of the mechanisms responsible for the various behaviors (Gowan et al. 1994) and their evolutionary significance require further examination.

Movements of cutthroat trout appear variable in space and time, may depend on season and climatic conditions, and may be sporadic (Brown and Mackay 1995), but little is known about movements during the harsh winter months. Evidence exists that mobile trout are of poorer condition than residents (brook trout; Gowan and Fausch 1996a) and cannot occupy optimal positions in the presence of residents (brown trout; Heggenes 1988). However, these findings were based on individuals over short spatial or temporal scales and not on individuals spanning longer intervals. The purpose of this chapter is to describe the seasonal and diel movement patterns of radio-tagged cutthroat trout, to compare these movements against capture data gathered from two-way traps, and to examine the relationship between the mobility strategies in relation to growth.

Study Area

Beaver Creek is a first-order stream in the Bear River Drainage, southeast Idaho, and

originates at 2400 m in elevation. It flows south for approximately 10 km before crossing

into Utah and continuing for another 9 km before it confluences with the Logan River.

Approximately 60 km of connected, passable stream exists before the first migration

barrier on the Logan River (Third Dam) is encountered. Beaver Creek contains self-

sustaining populations of stream-resident cutthroat trout and brook trout. The study

location occupies the uppermost 6 km of fish holding waters (Figure 2-1). Climatic

conditions at this altitude can be harsh with anchor ice and > 2 m of standing snow in

winter, overbank flows during the annual spring runoff, and summer droughts. Habitat

conditions include high gradient reaches with step pools under a forest canopy, low

gradient reaches that meander through meadows, and beaver ponds constructed largely

with willow (*Salix* sp.).

Materials and Methods

To assess seasonal movements of cutthroat trout, we captured adults by electrofishing

and surgically implanted them with 2.3-g, 40-MHZ radio transmitters. Fish were held

overnight so their condition could be checked after surgery, and then released into one of

three different habitat types: 1) high gradient ($> 3\%$ slope), 2) low gradient meadow ($<$

1.5% slope), or 3) beaver pond. Fish were located weekly to determine movements.

Because of transmitter size restrictions with our relatively small fish (< 200 g) and the

resulting short battery life of the transmitters (~ 90 days), we implanted fish during
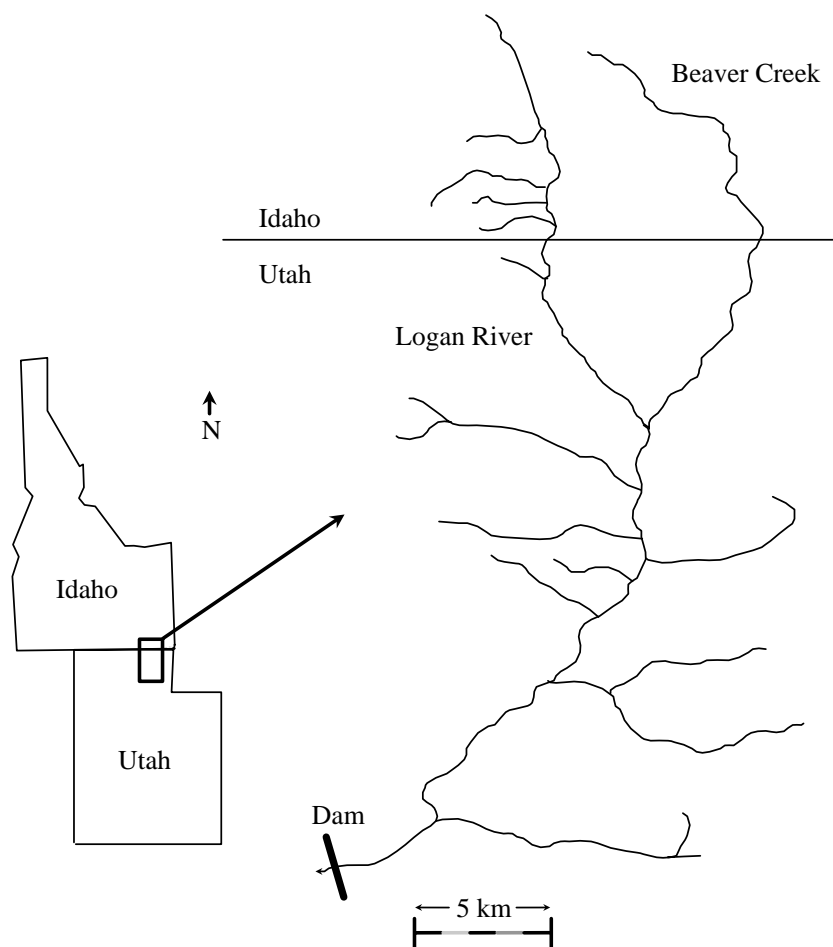
Fig. 2-1. Location of the study area on Beaver Creek, Idaho-Utah.

different seasons: 8 trout in summer 1995 released July 12, 7 for autumn 1995 released

August 31, and 9 in winter/spring 1995-1996 released December 1. For fish implanted

for the winter/spring trial, we had the transmitter pulse rate lowered from 45 to 30 pulses

per minute. This extended the battery from ~90 days to over 190 days, and allowed us to

follow the same fish through winter and spring 1996. Weather conditions and logistical

complications allowed only monthly tracking during winter and early spring and

prohibited travel to the site during May. Fish were located by triangulation with a

directional loop antenna. We recorded location, habitat type, use of cover, and position in

the channel for each fish. Each fish's UTM (universal transverse meridian) coordinates

were determined by using a 10-minute averaging session with a global positioning system

(GPS). The spatial accuracy of GPS determined coordinates was limited, but within 100

m. On September 7, 1995, we tracked 11 fish (6 summer implanted fish and 5 autumn

fish) throughout a 24-hour cycle, locating each individual hourly to determine daily

activity patterns. Observations on this date allowed us to catch the 2-week overlap

between summer and autumn radio-tagged fish. Distances moved during this period were

determined with a measuring tape. We defined home range as the distance between the

most upstream and most downstream positions.

In 1995, we used two-way traps to monitor the magnitude, timing, and direction of

trout movements, and to corroborate/validate the radio telemetry data. We installed three

traps at roughly 2.5-km intervals in the stream. These traps were capable of capturing

large numbers of all size and age classes of trout. Traps were checked daily from early

July through mid-November until maximum daily water temperatures fell below 2° C and ice formation limited trap function. All captured individuals were implanted with 11-mm passive integrated transponder (PIT) tags, of which each carried a unique identity code. Fish were weighed, measured, and released in the direction they were traveling at the time of capture. Additional fish were captured by electrofishing and hook and line throughout a 5-km reach in order to seed all three major habitat types with tagged fish. Marked individuals were released at or near their point of capture. Locations of tagged fish and the traps (UTM coordinates) were determined using a GPS. We PIT tagged and released 200 trout (167 cutthroat and 32 brook) during the summer of 1995. During summer 1996, we intensively electrofished a 7-km reach encompassing all PIT tag releases and less intensively sampled an additional 6 km of stream adjacent to the study area in pursuit of tag returns. We weighed, measured, released, and determined locations of recaptured fish with a GPS and distances moved were later calculated in ARC/INFO using the stream coverage for Beaver Creek. Fish recaptured greater than 100 m away from their point of release were categorized as moving while those within the 100 m were considered sedentary.

We tested seasonal differences in movements of radio-tagged cutthroat trout using the Wilcoxon rank sum test, but because of a capture effect on movements for fish implanted with radio transmitters during summer, we excluded the first 10 days of movements from the analysis. The distribution of PIT tag returns was tested against a Poisson distribution for random dispersion using the chi-square goodness-of-fit test. Differences in growth

between habitats and the mobile and stationary fractions were tested using analysis of covariance with instantaneous growth as the dependent variable, habitat type or mobility component as the treatment level, and individual length as the covariate. Movements of PIT tag returns in relation to habitats was tested using the chi-square test. All analyses were considered significant at $P < 0.05$.

Results

Movements of radio-tagged cutthroat trout varied among individuals and seasons, but some patterns emerged. Total distances moved during spring were significantly greater than during fall (Wilcoxon rank sum; P=0.021), winter (P=0.003), and summer (P=0.046), but were not significantly different between summer, fall, or winter (Figure 2-2). Only two individuals moved away from their point of release during autumn while the remaining six cutthroat were stationary. Both of these mobile fish did so during a 1-2 day period on different dates and then became stationary again. Autumn fish did not move. Individuals released in winter moved little from December-March (median = 0 m), but moved substantial distances during April-June (median = 576 m; Figure 2-3). During summer most fish moved immediately after release, but settled into a stationary pattern until the end of the monitoring period in mid-September. Median distance moved was 425 m, but only three fish moved after the first week (Figure 2-4).

Movement patterns of the summer and autumn radio-tagged fish were generally corroborated with the catches in the bidirectional weir traps. We captured 45 cutthroat and 27 brook trout in the two traps between July 9-November 7. While comparative
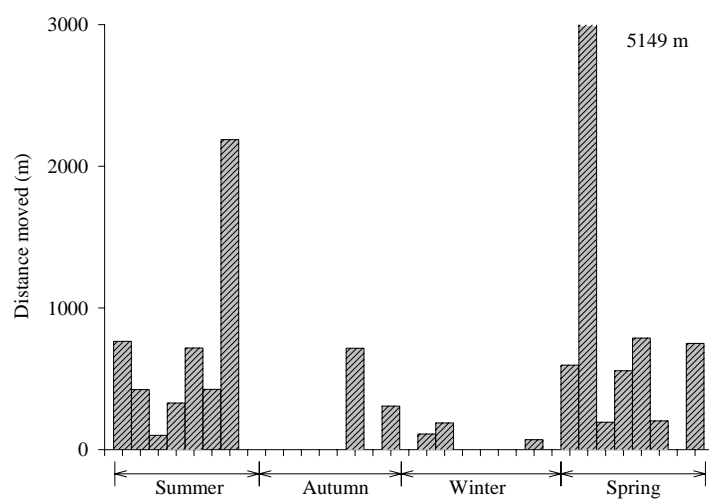
Fig. 2-2. Total distances moved by season for radio-tagged cutthroat trout. Each bar represents a seasonal observation for each individual fish.
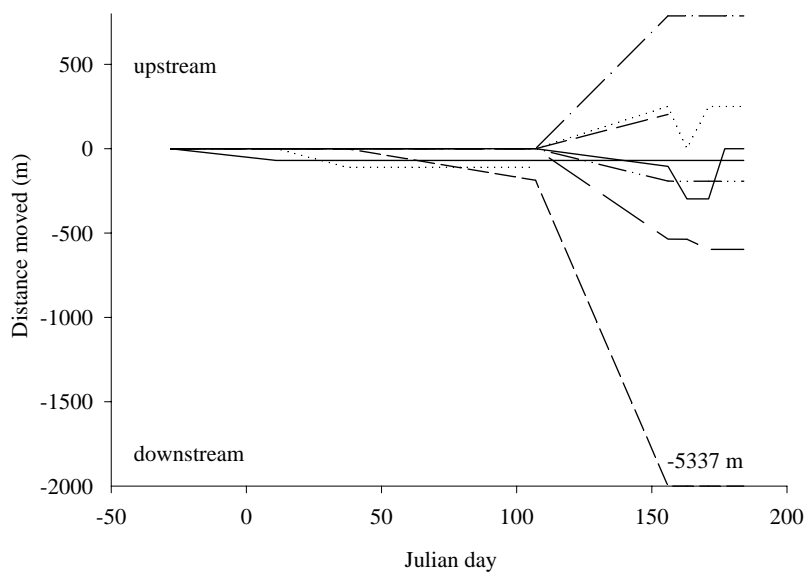
Fig. 2-3. Distances moved by Julian date for radio-tagged cutthroat trout followed from December 1995-June 1996. Values on the Y-axis indicate distances moved upstream (positive values) and downstream (negative values).
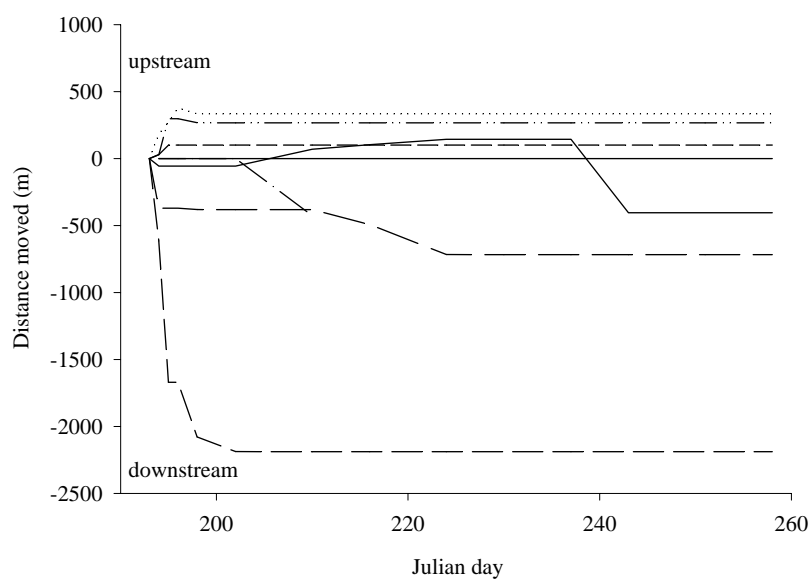
Fig. 2-4. Distances moved by Julian date for radio-tagged cutthroat trout followed from July 1995-early September 1995.Values on the Y-axis indicate distances moved upstream (positive values) and downstream (negative values).

statistical tests were not possible, the general patterns of movements between radio-tagged fish and free-ranging fish caught in the traps appear similar in magnitude and duration (Figure 2-5). Peak trout movements through traps occurred during mid-July and movement stopped almost completely by mid-August. This same pattern held for radio-tagged trout. There were no apparent directional trends in movements for radio-tagged fish (chi-square; $P = 0.79$), but trap data revealed a 4:1 upstream trend for cutthroat trout during July and August (chi-square; $P < 0.001$).

Although summer fish appeared mostly stationary after week 1, diel observations on September 7, 1995 showed that individual fish frequently moved during 24-hour periods. All summer fish moved at least twice during the diel period while only one of the five autumn fish moved. The average number of movements per fish was 3.8 for the 24 hour period, ranging from 0-13 movements. Distances moved per hour ranged from 0-121 m with a median distance of 36 m for movements greater than 0 m. Movement frequency was highest near dawn (500) and dusk (2100), slightly lower during daylight and lower still during darkness. Total distances moved during the diel period ranged from 0-259 m (median = 39 m) with home ranges between 0-60 m (median = 13 m; Figure 2-6). There was a positive relationship between total distances moved during a season and distances moved during the diel period suggesting that the more mobile individuals also made more local movements (Spearman rank correlation; $P < 0.001$).

We recaptured 26 of 167 (15.5%) PIT tagged cutthroat trout 1 year after their release and compared movements and growth rates. Thirteen of these recaptures were greater
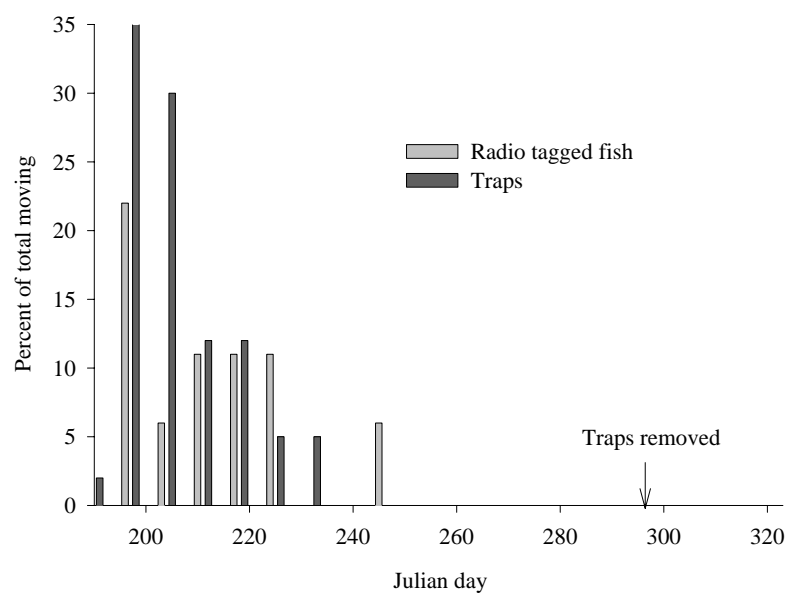
Fig. 2-5. Percentage of radio-tagged fish moving and fish captured in two-way traps by Julian date, July-early November 1995. Values are based on 65 telemetry observations and 43 fish captured in traps.
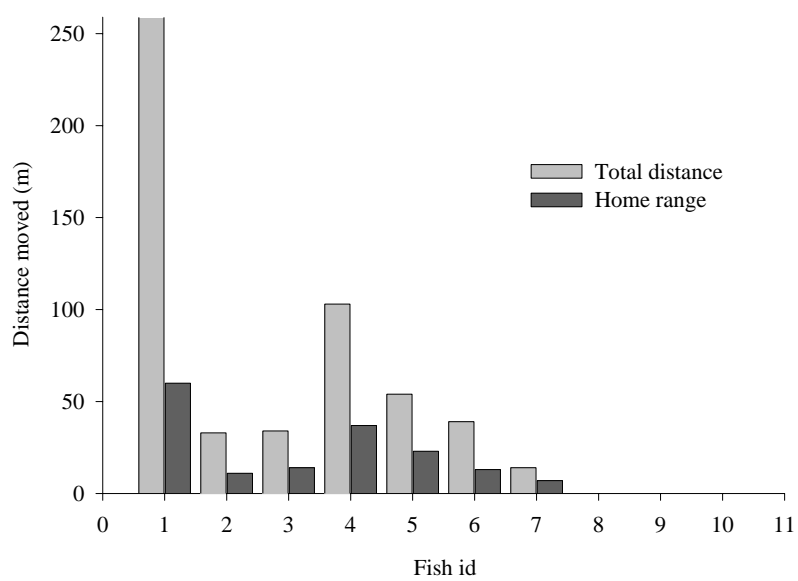
Fig. 2-6. Total distances moved and home ranges for 11 radio-tagged cutthroat trout located hourly during diel observations on September 7, 1995.

than 100 m away from their release point while the remainder were stationary (Figure 2-

7). Of the mobile fish, distances ranged from 109-3292 m (median = 797 m). The

distribution of distances moved was significantly different from a Poisson distribution

(chi-square; P<0.001) indicating a non-random dispersion pattern; there were more fish

than expected on both tails of the distribution. There was no significant

difference between instantaneous growth rates ($\bar{x} = 0.087$, SD=0.063) of the sedentary

and mobile portions (ANCOVA; P=0.42; Appendix Tables A-1, F1) and no differences in

growth among the high gradient, low gradient, and beaver pond habitat reach types for

either the stationary (ANCOVA; P=0.50; Appendix Tables A-2, F1) or mobile

(ANCOVA; P=0.11; Appendix Tables A-3, F1) portions. None of the habitat reach types

appeared more attractive to fish over the others; the proportions of each mobility

component were similar among habitats (chi-square; P=0.73).

Discussion

    There are two competing views about the relative superiority and fitness of the

stationary and mobile populations of fish. The first is that dispersing organisms are often

believed inferior in some way and are consequently forced from their home site (Stenseth

and Lidicker 1992). Nonresident brown trout were more often found in suboptimal

habitats in the presence of resident fish (Heggenes 1988), and emigrating red-spotted

masu salmon (*O. masou*) were in a significantly lower dominance rank than stationary

individuals (Nakano 1995), lending support to the inferiority of mobile individuals. If, as

suggested by the evidence, mobile individuals are inferior, these fish should have lower
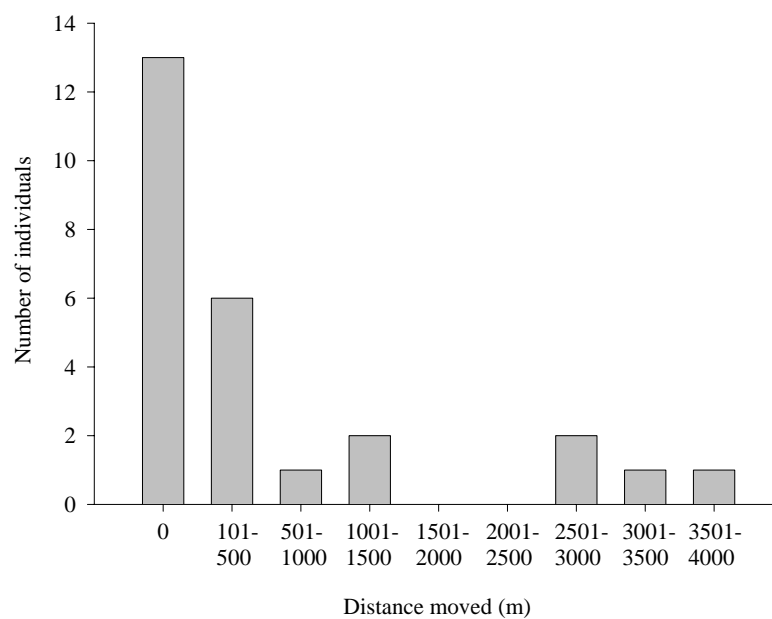
Fig. 2-7. Distribution of distances moved by PIT-tagged cutthroat trout captured over 12 km of stream one year after marking and release.

growth rates and presumably lower fitness than sedentary fish. Similarly, if environments fluctuate synchronously (as many streams do because of upstream-downstream linkages; Vannote et al. 1980), then unfavorable conditions at one site often mean unfavorable conditions at the other site too. Platts and Nelson (1988) reported within-stream population synchrony, but decreasing effect with distance. Recent work by Gowan and Fausch (1996a) suggest local and regional synchrony of adult brook trout population fluctuations. Site fidelity and stationarity might be superior to dispersal under these conditions (Stenseth and Lidicker 1992) because an individual is unlikely to find better conditions within dispersal distances. Specific individuals could not know this, but it could be an evolved response.

However, mobility is not necessarily a disadvantage, and may be favored in asynchronously fluctuating environments. Stream and regional trends might be deteriorating, but differing habitat reach types change at different rates (e.g., Kraft 1972). Mobility would enable organisms to track environmental conditions and take advantage of resources distributed patchily in space or time (food, habitat, mates, etc.). Mobility may also reflect the ability to successfully establish in new areas whereas sedentary individuals are not capable of invading and tracking resources. Under this line of thought, mobile individuals are superior and should exhibit greater growth.

Our growth rate results suggest that neither strategy is superior if growth is a sufficient indicator of individual fitness. Rather, we believe the population components to be alternative, equal, and flexible. From an evolutionary perspective, it would be

advantageous for some percentage of the population to be predisposed to dispersal to

hedge against locally unfavorable conditions and for genetic exchange, and for some

percentage to be predisposed to stationarity for the same hedging reasons. The remainder

of the population probably switches between the two behaviors, possibly depending on

local conditions or other unknown triggers. The radio telemetry (Figure 2-2) and the

distance frequency distribution of PIT tag recaptures (Figure 2-7) lend support to our

claims. So do most studies related to salmonid movements (Funk 1955; Harcup et al.

1984; Brown and Mackay 1995), including many cited in support of either stationarity or

mobility because these studies focused on modal values rather than on the distribution of

movements. Both the sedentary and mobile fractions were present in almost all cases, but

were emphasized to different degrees. Our data show both extremes and a continuum of

responses in-between.

The positive relationship between total seasonal distances moved and diel distances

moved suggests that within this gradient of variation, individual responses may be

somewhat rigid. This relationship is in opposition to observations of other researchers

(Harcup et al. 1984; Brown and Mackay 1995) who reported switching of movement

behaviors in individuals. Brown and Mackay (1995) found that cutthroat trout in the

Ram River, Alberta, were sedentary most of the time, but would move fairly long

distances in short periods before settling once more into a stationary pattern. We also

found this pattern in our weekly telemetry observations, but supplementing these data

with the finer resolution diel scale, the fixed individual movement pattern emerged.

However, our data are limited to one diel period and 11 individuals and more data are needed for a definitive answer.

The similarity in frequency and timing of movements between radio telemetry and two-way traps indicates that we obtained a representative sample despite the relatively small sample size of radio-tagged fish. Movements were most frequent during July and gradually tapered off until movement virtually ceased by early September. Young (1996) reported findings similar to this for Colorado River cutthroat trout (*O. c. pleuriticus*) and also reported no discernible directional trends for tagged fish (Young 1996; Young et al. 1997b). Although we found no trends in our tagged fish, we found an upstream trend for cutthroat trout caught in our two-way traps. Gowan and Fausch (1996b) also reported an upstream trend for brook trout even after modifying their traps to decrease escapement rates. We have no data on trap escapement, but both the downstream and upstream traps captured and held trout of all size classes. Directional migrations in response to dropping water temperatures have been reported elsewhere for cutthroat trout (Griffith and Smith 1993; Brown and Mackay 1995), but we found no movements through traps even as maximum daily water temperatures declined from 14° C down to 1° C when traps were pulled in November. Good fall and winter habitats were possibly nearby as in Chisholm et al. (1987) or this population may not undergo movements corresponding to dropping temperatures.

Gowan and Fausch (1996b) reported catching significantly larger fish in upstream traps compared to the general population over a 4-year period, and fish caught moving

downstream were longer in length than the general population but shorter than upstream movers. Their mobile fish had significantly lower condition than the general population. We found no difference in length of upstream versus downstream caught trout, but lacked the data for comparisons against the general population. However, growth rates measured from our PIT tag recaptures indicated no difference between the mobile and resident population fractions.

A surprisingly large amount of movement was found during the diel observations, even for fish settled into a stationary period based on weekly observations. These findings are similar to Matthews (1996) and Young et al. (1997a,b), who reported varying, but non-zero home ranges up to 352 m. Fish generally moved more during daylight hours with most movements occurring at dawn, dusk, and mid afternoon. Young et al. (1997b) reported greater cutthroat trout activity at mid day than at night and a positive relationship between activity and light intensity. If fish movement parallels activity, then our results support those of Young et al. (1997b). We observed several fish during the diel observation feeding for hours in one location without moving to other areas. We also observed two fish that spent the night in beaver ponds, moved into faster waters to feed during daylight, and moved back to the ponds at night. Matthews (1996) observed similar back and forth behavior in a minority of California golden trout (*O. m. aquabonita*), but her fish also actively fed at night.

Conclusion

In our study, cutthroat trout exhibited a wide variety of behaviors ranging from complete stationarity to frequent and wide-ranging movements. These patterns existed at seasonal, weekly, and diel scales and within individuals. When phrased as to whether stream-resident trout are sedentary or mobile, the answer is a resounding yes, both, and either. A polarized dichotomy does not exist; rather, they are ends of a continuum of behaviors expressed by the population. The modal value of the population probably depends on the quantity and quality of stream habitat, stream invertebrate productivity, and the presence of competitors. We should therefore manage populations for the inclusion of the tails of the distribution and use the mode as a possible diagnostic of stream condition. Higher proportions of mobile fish could indicate decreased quality or degrading environmental conditions. As available aquatic space becomes ever more limited and fragmented, it is imperative that we maintain enough stream for the population and not the individual because the long-term consequences of restricted space are not yet known. We speculate with evidence of restricted movements above barriers (Young 1996) that the stationary population fraction may be directionally selected for in small stream fragments. The long-term effects on genetic diversity and the ability of populations to recolonize after disturbance are unknown, but must be considered for the future.

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CHAPTER 3

INTERACTIONS BETWEEN NON-NATIVE BROOK TROUT

AND BONNEVILLE CUTTHROAT TROUT:

EVIDENCE FOR COMPETITION?[2]

Abstract.   Cutthroat trout have been eliminated from many of their native streams because of the introduction of non-native brook trout. In the few streams where the two species do coexist, cutthroat trout are typically restricted to high gradient reaches while brook trout inhabit the lower gradient sections. Beaver Creek in southeastern Idaho-Utah represents such a scenario. We used radio telemetry to conduct a series of experiments designed to test the strength of intra- and interspecific interference competition among high gradient, beaver pond, and low gradient reach types. We also sampled invertebrate drift and trout stomach contents to assess diet overlap and food availability for the two species among the reach types to determine the possibility of exploitative competition.

When cutthroat trout were the first to establish residence in enclosed stream sections, the experimental addition of fixed numbers of brook trout as competitors had less effect in displacing the established residents than the same numbers of cutthroat. This effect did not differ between reach types despite brook trout excluding cutthroat trout in beaver ponds and low gradient reaches in the wild. Resident cutthroat were displaced at relatively low densities during the first two trials, but the densities required for

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displacement increased in the two later trials. When the residents were removed and then

reintroduced into sections already containing brook or cutthroat trout competitors, the

residents were able to establish successfully in only 20% of the trials. Neither reach type,

species of competitor, nor size of the invader influenced the chance of successful re-

establishment. Brook and cutthroat trout in allopatry used similar stream positions in 8 of

10 trials, but the frequency distributions of stream positions used by each species differed

in 8 of 10 trials when in sympatry. While this implies mutual displacement, brook trout

in sympatry used habitat features similar to brook trout in allopatry. Conversely,

cutthroat trout in sympatry switched their habitat use in 4 of 10 trials to occupy positions

not previously selected for when allopatric. Competition for food probably does not

occur because food does not appear to be limiting, but there may be exploitative

competition by brook trout in beaver ponds where the dominant food items for each

species were consumed at levels exceeding availability in the drift samples.

INTRODUCTION

Introductions of exotic fish species have resulted in restricted ranges and replacement

of native fishes throughout the world. The most notorious example is the Nile perch

(*Lates nilotica*) introduction to Lake Victoria, Africa, that resulted in the elimination of

over 200 species of cichlids (Witte et al. 1992). The introduction of tucanare (*Cichla

ocellaris*) to waterways of Panama resulted in the elimination of several native species in

Gatun Lake (Zaret and Paine 1973). European brown trout (*Salmo trutta*) and rainbow

trout (*Oncorhynchus mykiss*) introductions have resulted in the reduction or elimination

of many native galaxiid fishes in New Zealand (Crowl et al. 1992, McIntosh et al. 1992)

and modified native fish communities globally (Fausch 1988), while the sea lamprey

(*Petromyzon marinus*) invasions of the Laurentian Great Lakes decimated lake trout

(*Salvelinus namaycush*) populations (Lawrie 1970) .

Non-native introductions have also deleteriously affected stream-resident salmonid

species in North America. Rainbow trout, native to the west coast drainages of North

America, are eliminating brook trout (*Salvelinus fontinalis*) populations in the

southeastern United States from their native range (Larson and Moore 1985). Brown

trout, native to Europe, have also been shown to eliminate brook trout (Waters 1983). In

the interior western United States, brook trout have eliminated the native cutthroat trout

(*Oncorhynchus clarki*) from most streams where they have been introduced in

Yellowstone National Park (Varley and Gresswell 1988) and other areas (Moyle and

Vondracek 1985, Fausch 1989).

Mechanisms for the elimination of one species by another can include predation

(Savidge 1987), environmental modifications (Bettoli et al. 1991), hybridization (Tol and

French 1988), exploitative competition (Tilman et al. 1981), and interference competition

(Connell 1961). Circumstantial evidence exists within the salmonid literature on species

eliminations, but direct evidence and the underlying mechanisms are often unclear

because few studies have been adequately designed to test for specific mechanisms

(Fausch 1988). Predation of other fish is rare within stream-resident salmonid

communities; diet studies rarely report fish in stomach contents (e.g., Fleener 1951,

Griffith 1974, Allan 1978, Hubert and Rhodes 1989, Young et al. 1997). Similarly,

salmonids do not modify the surrounding environment except for channel substrates

during a brief spawning period. Hybridization between cutthroat and rainbow trout

jeopardizes many cutthroat trout populations (Liknes and Graham 1988, Tol and French

1988) while introgression by non-native brook trout may threaten bull trout populations

(Leary et al. 1983). However, interbreeding between other species is very rare.

Exploitative competition among salmonids for food is possible, but not well documented.

Similarly, interspecific competition in salmonids has been relatively hard to prove,

although it is a likely mechanism. Fausch and White (1981) demonstrated shifts in

habitat use by brook trout after removal of the dominant brown trout in a Michigan

stream, and is probably the best experimental evidence of interspecific competition in this

group of fishes. Other studies appear less conclusive or result in patterns counter to those

drawn from species distributions in the wild. For example, Griffith (1972) found

underyearling brook trout to dominate cutthroat trout of the same size in laboratory

experiments. In older age classes, cutthroat trout were more aggressive and could not be

displaced by similarly aged brook trout. However, results similar to these have not been

documented in wild populations.

As with other organisms (Connell 1961, Park 1962), the outcome of competition

experiments with stream-dwelling salmonids may be confounded by changing

environmental conditions typical of streams. Cunjak and Green (1984) reported

dominance of brook trout over rainbow trout in slow velocities, but higher current velocities resulted in equal competitive abilities. Increased water temperatures in a laboratory experiment shifted the competitive balance between brook trout and cutthroat trout from neutral to brook trout dominance (De Staso and Rahel 1994) and may be true in other trout species comparisons (Fausch 1988). Similarly, distribution patterns of coexisting populations of stream-dwelling competitors are often segregated by stream gradient with the inferior species often restricted to higher gradient reaches and the dominant species in lower gradient areas (Griffith 1972, Larson and Moore 1985).

In streams where brook trout and cutthroat trout do coexist, brook trout typically predominate in beaver ponds and the lower gradient reaches while cutthroat trout occupy higher gradient reaches (Bachman 1958, MacPhee 1966, Griffith 1972). The purpose of this chapter is to attempt to define the mechanisms of species' replacement to explain the species distribution in Beaver Creek, a mixed gradient stream in southeast Idaho and northern Utah. Our objectives were to: (1) examine the potential for exploitative competition between brook and cutthroat trout; (2) determine the relative strengths of intra- and interspecific interference competition on cutthroat trout; and (3) determine the effects of the order of arrival on the ability to establish residency in cutthroat trout. We attempted this through comparison of food availability and diet contents of the two species and through density manipulation experiments within large-scale stream enclosures.

METHODS

Study site description and location

Beaver Creek originates in southeast Idaho and flows south for approximately 10 km before crossing into northeast Utah to its confluence with the Logan River 9 km downstream of the state boundary. It is a first-order stream originating at 2400 m in elevation and is sustained by ground water during summer and autumn after snowmelt. The stream is usually at base flow from mid-July until late winter. Beaver Creek contains self-sustaining populations of native Bonneville cutthroat trout (*O. c. utah*) and eastern brook trout. The stream receives little fishing pressure and strict regulations prohibit the keeping of cutthroat trout under 16 inches. The study area is bounded on both ends by sections of higher gradient step pools flowing through coniferous forest and shrubs, with low gradient meanders through meadows and beaver ponds constructed with willow (*Salix* sp.) and aspen (*Populus tremuloides*, Fig. 3-1). Channel slopes in the high gradient reaches were 3-5%, < 1.5% in low gradient reaches, and < 0.5% in beaver ponds where current velocities were very slow (Fallau 1995).

Measurement of food and growth

We examined the extent of diet similarity and the potential for exploitative competition between brook trout and cutthroat trout by sampling invertebrate drift and

Length = 5.8 km

High Gradient Reach

Brook Trout

Cutthroat Trout

Beaver Ponds

Low Gradient Reach

High Gradient Reach
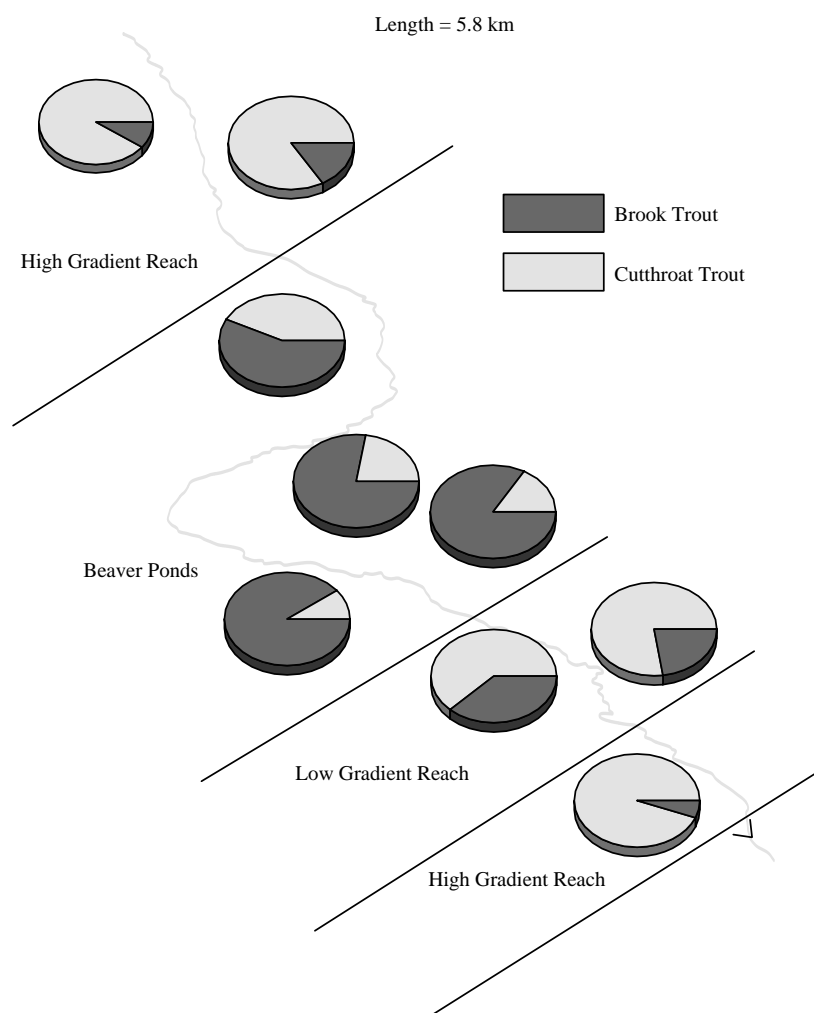
Fig. 3-1. The distribution of brook and cutthroat trout in the 6-km study section of Beaver Creek, Idaho.

trout stomach contents in late August 1995. In each habitat reach type, we collected three

1-hour drift samples and later identified contents to family when possible. On the

same day and in the same areas, we collected stomach contents from 26 brook and 81

cutthroat trout by gastric lavage, a nonlethal technique. Invertebrates in the preserved

stomach contents were later identified to order where possible. Diet overlap was

calculated by taking the minimum percentage of a taxon in the diets of brook and

cutthroat trout and summing this percentage for all taxa in the diet. Growth between

species was compared using ANCOVA with length as the covariate, using data from PIT

(passive integrative transponder) tagged trout recaptured (5 brook trout and 26 cutthroat

trout) by electrofishing one year after initial tagging and measurement (see Chapter 2).

Density and displacement—experiment 1

We conducted the first series of experiments during summer 1996 to determine: (1)

the strength of intra- and interspecific interference competition in cutthroat and brook

trout; (2) the influences of habitat on these interactions, and (3) the ability of cutthroat

trout to invade and establish in a stream already containing fish. To complete these

objectives we employed an additive and substitutive design. We established 9

experimental stream sections 15-30 m in length: three in the high gradient reach type,

three in the low gradient reach type, and three in beaver ponds. We blocked fish passage

by installing a 19-mm diameter plastic mesh fence at the top and bottom of each section

and removed all fish by total depletion electrofishing. Stakes placed along the

streambank subdivided each section linearly into a series of 3-m sections and

longitudinally across the stream into left margin, midchannel, and right margin. This

formed a grid of cells used for recording fish positions. For each cell in every section, we

visually estimated dominant and subdominant substrate particle sizes and water velocity,

measured the minimum, mean, and maximum water depth and channel complexity (the

ratio of the perimeter of the stream bed to a straight line distance), recorded the number of

rocks potentially serving as cover for fish, and recorded the presence of undercut banks,

overhead cover, and the number of pieces of wood longer than 1 m and > 5 cm in

diameter (Appendix C, Fig. C-1, Tables C-1 through C-19).

   We anesthetized nine cutthroat trout 220-280 mm in length with tricaine

methanesulfonate (MS-222) and surgically implanted 2.3-g 40-MHZ radio transmitters.

Tagged fish were held for 24 hours and then used in the experimental trials. We

introduced a single, randomly selected, radio tagged cutthroat trout into each section.

These fish were termed the "residents." We located each of these resident fish hourly for

at least 10 hours every day and recorded the cells in the stream grid they occupied. The

residents were allowed to acclimate undisturbed for 3 d. This established a baseline of

preferred feeding and resting areas for each fish in a given section and was used for

comparison with feeding and resting areas occupied in the presence of competitors. At

the end of day 3 and each day thereafter, five fish within the same size range (but without

radio transmitters) as the residents were introduced into each section. We continued to

locate the resident in each section hourly each day to determine if displacement occurred.

The final day (day 7) of each trial ended with each section containing the resident and 20 introduced competitors. This maximum density on day 7 was 2-4 times the maximum ambient density of fish naturally occurring within the sections before experiments began. We conducted four trials in each section; two trials used cutthroat trout as the added competitor whereas the other two trials used brook trout. A different, randomly chosen resident was used for each trial. At the end of each trial, all fish were removed, a new resident placed into the section, and a new trial started the following day.

Data were analyzed with log-linear models using the GENMOD procedure in SAS 6.12 by comparing the distribution of habitat use of residents during the three day acclimation against their distributions for a given competitor density. The density (if any) at which habitat use differed significantly from the acclimation period was termed the threshold density. We tested for intra- and interspecific effects and for habitat effects by ranking threshold densities (because the densities were ordinal) and performed an ANOVA on the ranks—the equivalent of Friedman's test.

Ordering effects — experiment 2

We examined the effect of order of arrival on invasion ability of cutthroat trout by using an experimental setup similar to the one described above. After the competitor addition trials ended, we left the 20 competitors in every section, but removed the resident radio-tagged cutthroat trout. We then repeated the experiment described above using the same residents in the same sections in the same order, but competitors were

already present within all sections. The residents were thus forced to invade a saturated

environment. We conducted four ordering effects trials in each of the nine sections.

Residents were located hourly for 2 d, removed, and a new trial started with a new

resident fish.   We analyzed these data using Fisher's exact test in a pairwise comparison

of distributions of cells used in the ordering effects trial against the distributions in the

acclimation period of the competitor addition trial used by the same fish.

Niche shifts and segregation — experiment 3

During 1997 we conducted a second experiment designed to test for interference

competition through displacement. We implanted 10 cutthroat trout and 10 brook trout

with radio transmitters using the same techniques described earlier and established 10

fenced sections 12-15 m long in the low gradient reach habitat of Beaver Creek. Each

section was mapped and divided into cells as described earlier and all fish were removed

by electrofishing. In each section we introduced four radio-tagged trout, located them

hourly for 45 continuous hours, and recorded their locations. We conducted three trials in

each section: allopatric cutthroat trout, allopatric brook trout, and a sympatric

cutthroat/brook trout (two of each species) trial. At the end of each trial, the radio-tagged

fish was removed and another trial initiated. For each trial, we pooled habitat

distributions of all fish to compare allopatric brook trout versus allopatric cutthroat trout

versus sympatric trials using log-linear models.

For each section, we used stepwise logistic regression to build habitat models for allopatric cutthroat, allopatric brook, and for each species in the sympatric trials. These models were used to detect the occurrence of niche shifts due to interference competition. Variables used in the regression analysis were water velocity, channel complexity, mean, minimum and maximum water depth, presence of undercut banks, presence of overhead cover, large woody debris, and rocks potentially serving as cover within each cell. We report only those variables that increased the odds of stream position selection or avoidance by 1.5 or greater. All analyses were considered significant at $P < 0.05$.

RESULTS

Food abundance, diet overlap, and growth
of brook and cutthroat trout

Diets of brook and cutthroat trout overlapped to moderate degrees in each reach type, but consumption of specific taxa was rarely greater than its availability in the drift samples (Table 3-1, Appendix Table D-1). Overlap was greatest in the high gradient reach type where the two species shared 75% of their diets. Terrestrial insects comprised the majority of the diet content for both species (cutthroat=57%, brook=61%), but cutthroat trout used this resource to a much greater extent than did brook trout, consuming almost 2.5 times more terrestrial organisms than were available in our 1-hour drift samples (Table 3-1). In contrast, brook trout consumed terrestrials well below their availability in the drift.

Table 3-1. Relative contribution of various taxa to diets of brook and cutthroat trout, food availability (measured from drift samples) relative to consumption, and diet overlap between the two species.

		Percent of diet						
Species	Section	Ephemeroptera	Plecoptera	Trichoptera	Terrestrial	Dipteran larvae	Dipteran pupae	Coleoptera
Cutthroat	Beaver pond	0.74	0.00	0.57	10.45	55.84	29.71	1.00
Cutthroat	High gradient	4.95	0.64	7.95	57.29	24.81	2.00	0.82
Cutthroat	Low gradient	2.73	0.11	0.89	49.11	45.16	1.16	0.32
Brook	Beaver pond	0.33	0.00	5.27	11.20	17.47	62.54	1.67
Brook	High gradient	0.57	0.00	14.77	60.80	7.39	1.14	14.20
Brook	Low gradient	4.02	1.01	11.06	15.08	46.23	18.59	1.01

		Percent of diet relative to food availability						
Species	Section	Ephemeroptera	Plecoptera	Trichoptera	Terrestrial	Dipteran larvae	Dipteran pupae	Coleoptera
Cutthroat	Beaver pond	8.33	0.00	100.00	248.30	99.23	621.00	350.00
Cutthroat	High gradient	20.80	58.33	68.36	213.01	15.96	15.49	15.52
Cutthroat	Low gradient	21.67	5.56	47.22	343.38	21.56	8.59	7.14
Brook	Beaver pond	1.08	0.00	262.50	76.14	8.89	374.00	166.67
Brook	High gradient	0.19	0.00	10.16	18.07	0.38	0.70	21.55
Brook	Low gradient	3.33	5.56	61.11	11.03	2.31	14.45	2.38

	Percent diet overlap							
Section	Ephemeroptera	Plecoptera	Trichoptera	Terrestrial	Dipteran larvae	Dipteran pupae	Coleoptera	Total overlap
Beaver pond	0.33	0.00	0.57	10.45	17.47	29.71	1.00	59.56
High gradient	0.57	0.00	7.95	57.29	7.39	1.14	0.82	75.15
Low gradient	2.73	0.11	0.89	15.08	45.16	1.16	0.32	65.44

Diet overlap between the two species dropped to 65% in the low gradient reach type (Table 3-1) where terrestrial organisms (49%) and dipteran larvae (45%) were the dominant food items for cutthroat trout, while brook trout fed most heavily on dipteran larvae (46%), dipteran pupae (18%), and terrestrials (15%). Cutthroat trout again consumed substantially more terrestrials than were present in the drift samples while all remaining taxa were consumed by both species at levels well below their presence in the drift.

Cutthroat and brook trout sampled in beaver ponds exhibited the lowest degree of diet overlap between the species (60%). The same three taxa, dipteran larvae, dipteran pupae, and terrestrials, were dominant in both species' diets, but importance shifted from dipteran larvae in cutthroat trout (56%) to dipteran pupae for brook trout (63%, Table 3-1). Diet contents relative to drift availability showed cutthroat in beaver ponds consuming many more dipteran pupae and terrestrials than were available, while they consumed as many dipteran larvae as were found in the drift. Similarly, brook trout consumed many more dipteran pupae than were available and also consumed a large percentage of terrestrials relative to drift availability.

Growth rates based on PIT tagged fish marked in summer 1995 and recaptured during summer 1996 showed no significant differences between species (ANCOVA, P = 0.64, Appendix Tables A-4, F1). Although variability was high and sample size was low for brook trout, both species exhibited the same ranges of values. We also found no

significant differences in food availability based on our drift samples among the three reach types (ANOVA, P = 0.66, Appendix Tables B-1, F1).

Density thresholds

Density thresholds existed and differed depending on the species of competitor added, but a time effect complicated matters. Threshold densities for a given section were usually 5 or 10 competitors during trial 1, increased slightly for trial 2, and increased enough during trials 3 and 4 that the tagged residents of most sections during trial 4 did not change habitat positions or behaviors when compared against the 3-day acclimation period. Cutthroat competitors displaced the resident radio-tagged cutthroat trout at lower densities than brook trout competitors, but the result was not statistically significant (ANOVA, P = 0.10, Appendix Tables B-2, F1). Habitat reach type had no effect on threshold density (ANOVA, P = 0.85, Appendix Tables B-3, F1) and did not change through time. When each habitat reach type was analyzed separately, again no significant differences between species existed within any reach type (Appendix Tables B-4, B-5, and B-6), but intraspecific effects were nearly significant in high gradient reach types (ANOVA, P = 0.13, Appendix Tables B-6, F1).

Ordering effects

Order of arrival appears important in the ability of individuals to establish in areas already containing fish. Despite having previously sampled and established stations in

the experimental sections, the resident radio-tagged cutthroat trout used the same areas as

during the acclimation period in only 5 of 31 (16%, Appendix E) trials. Neither reach

type nor species of competitor appeared to influence a resident's chance of successfully

invading a section. Similarly, there was no difference in the ability of individuals to

successfully establish in sections; the most successful resident established in only two of

four trials. These analyses were based on comparing stream position use in the ordering

effects trials against the same individual's stream position use during the 3-day

acclimation period of the competitor addition trials using Fisher's exact test. Comparing

the number of movements between the two experiments revealed few differences in

movement frequency; only 8 of 31 (27%) ordering effects trials resulted in significantly

more movements compared to the acclimation period of the competitor addition trials.

Displacement and niche shifts

Brook and cutthroat trout behaved similarly in allopatry, but exhibited mutual

displacement when in sympatry. When in allopatry, brook trout and cutthroat trout used

similar stream positions in similar frequencies in 8 of 10 trials (log-linear analysis).

However, sympatric brook and cutthroat trout differed significantly in use of stream

positions relative to their allopatric counterparts in 8 of 10 trials for brook trout and in 8

of 10 trials for cutthroat trout.

We further explored these data by analyzing daylight and night readings separately to

examine whether interactions occurred at feeding areas which are occupied during

daylight or in resting areas occupied at night. Allopatric brook and allopatric cutthroat trout used similar stream positions during daylight where they differed significantly in use in only 2 of 10 sections (log-linear analysis). In contrast, the two species differed significantly in 5 of 10 sections in their night time use of stream positions when in allopatry. Similarly, comparison of sympatric brook or cutthroat trout with their respective allopatric counterparts resulted in no clear patterns; we detected significant differences using log-linear analysis in roughly half of the 10 sections for all comparisons both for daylight and dark.

Despite allopatric brook and allopatric cutthroat trout using statistically similar stream positions in 8 of 10 sections, logistic regression results typically identified only one variable shared between the species for any given section, and it was often a different variable depending on the section (Table 3-2). However, we should expect this because not all habitat was present in the same quantities or configurations among sections. Brook trout alone and sympatric with cutthroat tended to select for the same habitat features despite their frequencies of use being different. Conversely, cutthroat trout sympatric with brook trout changed their use of habitat features in sections 2 (undercut banks), 3 (overhead cover), 4 (LWD), and 6 (channel complexity) compared with selections when cutthroat were in allopatry (Table 3-2). This suggests that some sort of displacement is occurring when cutthroat trout are sympatric with brook trout. Additionally, in three of these same sections, the sympatric brook trout selected for the same habitat features as the allopatric cutthroat, but avoided by the sympatric cutthroat.

Table 3-2. Logistic regression list of significant variables and their influence (+ =
selection for; - = selection against) on the selection of stream positions of allopatric
cutthroat trout, allopatric brook trout, cutthroat trout sympatric with brook trout, and
brook trout sympatric with cutthroat trout in the 10 experimental exclosures. All
variables listed were significant at $P < 0.05$ and had odds ratios increasing selection or
avoidance of a stream position by 1.5 times or greater. All variables run from smaller
to larger (e.g. flow velocity running from slow to fast).

	Allopatric cutthroat	Allopatric brook	Sympatric cutthroat	Sympatric brook
Section 1	+ substrate	- substrate	- maximum depth	- maximum depth
	+ LWD	- channel complexity		
Section 2		- channel complexity		- channel complexity
		- cover rocks		+ undercut bank
	+ undercut bank	+ undercut banks	- undercut bank	+ overhead cover
	+ overhead cover	+ overhead cover	+ overhead cover	
Section 3		- flow velocity		- flow velocity
		+ substrate	- substrate	+ substrate
		+ channel complexity	+ maximum depth	+ channel complexity
	+ undercut bank	- cover rocks	- overhead cover	- cover rocks
	+ overhead cover			
Section 4	+ channel complexity			nothing
	- LWD		+ LWD	
	+ undercut banks	+ undercut banks	+ undercut banks	

Table 3-2 (continued)

	Allopatric cutthroat	Allopatric brook	Sympatric cutthroat	Sympatric brook
Section 5		- substrate	+ substrate	
		+ channel complexity	+ channel complexity	
		- cover rocks	- cover rocks	- cover rocks
	- LWD	- LWD		
Section 6	- substrate	- substrate		
	+ channel complexity	+ channel complexity	- channel complexity	+ channel complexity
		+ LWD	+ minimum depth	
	+ undercut banks	+ undercut banks	- maximum depth	
Section 7	+ channel complexity	+ channel complexity	- substrate	- average depth
	- cover rocks		- cover rocks	+ maximum depth
	- LWD			
	+ overhead cover			+ undercut banks
		+ undercut banks	+ undercut banks	
Section 8	+ LWD	+ LWD	+ LWD	+ LWD
Section 9	nothing	nothing	nothing	nothing
Section 10	- maximum depth	nothing	- maximum depth	- maximum depth

DISCUSSION

Cutthroat trout in Beaver Creek predominate in high gradient reaches, brook trout in beaver ponds, and a roughly equal mix exists in low gradient reaches. If interspecific interference competition produced this distribution pattern, we would expect a significant effect of brook trout and also a difference among reach habitat types. There was neither a difference in threshold densities among the high gradient, low gradient, or beaver pond reach types nor were the threshold densities lower when brook trout were the added competitors. The residents actually maintained a higher threshold density in the presence of brook trout compared to cutthroat trout. While the result was not statistically significant, we feel that it reflects the relative magnitude of intra- versus interspecific interactions in mature individuals when cutthroat trout are the first to establish in an area.

Threshold densities were relatively low during the first trial but progressively increased with each trial. This could be the result of residents losing strength and dominance rank after surgical implantation of transmitters and becoming progressively stronger with time, but recent work has demonstrated no change in social position due to surgery (Swanberg and Geist 1997) and minimal physical effects (Martin et al. 1995). Rather, we believe that the increase in threshold density with time resulted from residents learning and adapting to restricted movements and limited habitat availability within the enclosures. During the acclimation period, residents were able to choose any habitat. It is possible that once competitors were added, residents quickly gave up their positions to find other areas without competitors since the residents had spent the previous 3 days in

areas without any other competitors. However, competitor densities increased daily; the residents lost possession of their preferred areas and could not escape to areas with lower competitor densities. After one or two trials with this happening, the residents possibly anticipated that this would happen again and they began holding territories more vigorously.

The order of arrival in territorial organisms determines the outcome of many interactions involving space because prior residence typically confers an advantage (Jenkins 1969, Sale 1978, Heggenes 1988). When cutthroat trout were allowed to establish first, they presumably occupied the preferred positions within any section because dominant individuals occupy optimal positions (Fausch and White 1981, Nakano 1995). When these same individuals were removed and then reintroduced back into the same sections now containing competitors, they were unable to establish in those same areas. This is probably because both brook and cutthroat trout form stable dominance hierarchies and establish and vigorously defend territories against intra- and interspecific intruders (Griffith 1972, Diana and Lane 1978, Grant et al. 1989). The added competitors were probably occupying the most energetically preferable spots and excluded the reintroduced residents. Heggenes (1988) reported resident brown trout excluding nonresident brown trout from preferred areas and into suboptimal stream positions. Neither the species of competitor, the reach type, nor the size of the reintroduced resident made a difference in invasion success, making the situation similar to Sale's (1978)

lottery model for reef fishes where the first individual to settle an area holds a distinct competitive advantage over invaders.

In our study, cutthroat trout sympatric with brook trout were often relegated to areas they did not select when in allopatry. Although the use of stream positions by both brook and cutthroat trout in sympatry differed statistically from their respective allopatric trials, brook trout generally used the same types of habitat features in both the allopatric and sympatric trials. In contrast, cutthroat changed preferences in 4 of 10 sections. These niche shifts in cutthroat trout appear counter to the results of the competitor addition experiments where cutthroat trout resisted displacement by brook trout. We feel that order of arrival explains this paradox. In the competitor addition experiments, cutthroat trout were allowed to establish residency within a section for 3 days before any competitors were added. This probably enabled them to successfully hold territories in preferred areas until densities became great enough that they were either displaced or expended too much energy towards territorial defense. In the displacement experiments, however, individuals of both species were not able to establish prior residence, but were forced to establish a territory in the presence of other individuals also trying to establish territories.

Niche shifts are not uncommon between salmonids that did not evolve together when they are forced into sympatry. Gatz et al. (1987) reported rainbow trout used preferred areas less when sympatric with brown trout than when in allopatry. Similarly, Fausch and White (1981) found that brook trout occupied energetically more costly resting areas in

the presence of brown trout compared to when brown trout were removed, while DeWald

and Wilzbach (1992) reported niche shifts in brook trout in the presence of brown trout.

Conversely, Griffith (1972) found no differences in habitat use of cutthroat trout

populations sympatric with brook trout and those in allopatry, but his results were based

on spatially separated cutthroat trout populations and did not directly test effects by

adding or removing species.

Despite our sections measuring 15-30 m long by approximately 4 m wide, fish were

still restricted in their ability to move and we cannot rule out cage effects. However, the

presence of numerous adult fish in all of the areas where we placed our sections indicates

that habitat was not limiting for the residents or for the first few competitors added.

Recent work has shown that while movement in stream-resident trout is greater than

formerly believed (Gowan et al. 1994, Young 1994, Gowan and Fausch 1996), a large

percentage still maintain restricted home ranges (Heggenes et al. 1991, Brown and

Mackay 1995). We cannot discount cage effects, but feel sections were probably large

enough to eliminate many problems posed by small enclosures.

Food and diets

Exploitative competition probably does not exist between brook and cutthroat trout in

Beaver Creek. Diet overlap ranged between 60-75%, but there still appears to be enough

available food and diet segregation to avoid exploitation. Food may be limiting in some

systems (Wilzbach et al. 1986, Ensign et al. 1990), but Beaver Creek is a very productive

stream. Brook trout do not appear to be inhibiting cutthroat trout from acquiring the

necessary nutrients because growth rates of cutthroat trout did not differ between areas

dominated by brook trout and areas containing few or no brook trout (Chapter 2).

We speculate that if exploitative competition does exist, it would probably occur in

beaver ponds. While diet overlap was least in these habitats, the most important food

items were similar between the species and were consumed at levels at or above their

availability in the drift. For these items, brook trout appeared to consume more than the

cutthroat trout. Brook trout inhabit slower velocity areas, whereas cutthroat trout

typically occupy higher velocity areas such as at the heads of pools (Griffith 1972).

While brook trout appear able to adapt their body morphology at a young age to live in

many different current velocity gradients (McLaughlin and Grant 1994), cutthroat trout

are more cylindrical shaped (Bisson et al. 1988) and possibly better adapted to higher

velocities than typically exist in beaver ponds. Cutthroat trout might be at a competitive

disadvantage in beaver ponds where they are forced to feed in low velocity environments

better suited to the deep bodied brook trout we found in beaver ponds in Beaver Creek.

Proposal for coexistence or replacement

Our results suggest that cutthroat trout are competitively equal with brook trout and

possibly dominant when they have prior residence. However, introductions of brook trout

typically eliminate cutthroat trout from their native streams. We propose a multi-step

process creating the distributional coexistence patterns or species replacement through

attrition. Where high gradient reaches exist, cutthroat trout can coexist with brook trout because the cylindrical shape of the cutthroat trout body morphology (Bisson et al. 1988) allows them to more efficiently exploit resources and space in these higher velocity areas. Additionally, prior residence allows cutthroat to successfully hold and dominate high gradient reaches. This provides a situation analogous to an inclusive niche (Miller 1967) where cutthroat trout can exploit a resource gradient unavailable to brook trout, but brook trout must share all resources with cutthroat trout in high gradient reaches.

Beaver ponds and some lower gradient reaches energetically favor brook trout because of their relatively deeper bodies and their opportunistic feeding mode that includes both benthos and drift. In contrast, the more cylindrical shape of cutthroat trout is adapted to faster currents and their almost exclusive consumption of invertebrate drift reduces the potential food available relative to brook trout. The low current velocities of beaver ponds might confer an advantage to brook trout and allow the possibility of species replacement.

Juvenile brook trout are more aggressive and dominate cutthroat trout of equal size (Griffith 1972, David J. Buys personal communication). Brook trout young-of-the-year are larger than cutthroat going into their first winter of life because the fall-spawned brook trout fry emerge before spring-spawned cutthroat. Larger size conveys dominance (Grant 1990) and higher overwinter survival (Hunt 1969). It is possible that brook trout young-of-the-year may exclude cutthroat from suitable positions making them more vulnerable to predation by older fish or causing them to expend more energy resulting in

reduced survival. Conversely, there may be no interspecific effect at all, but rather an attrition effect.

We speculate that a small advantage in overwinter survival due to larger body sizes of young-of-the-year brook trout or dominance in interspecific interactions could result in species replacement. When an available space is vacated (e.g., mortality, dispersal, etc.) by larger fish, the probability of that spot being occupied by a brook trout is incrementally greater than by cutthroat trout. Our niche shift experiments suggest that if an individual of each species arrives at the same time, the brook trout will win. Similarly, our ordering effects trials imply that cutthroat trout are unlikely to successfully displace individuals already holding territories. Therefore, any small advantage possessed by brook trout will result in a stepwise replacement in time through attrition. We stress that this is just a hypothesis. Future research in brook and cutthroat trout interactions should be directed at the juvenile stages to determine mechanisms of replacement or coexistence and management applications for cutthroat recovery.

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CHAPTER 4

CRITICAL NEEDS FOR CUTTHROAT TROUT

RECOVERY AND PERSISTENCE[3]

Abstract: Interior stocks of cutthroat trout (*Oncorhynchus clarki*) largely exist as populations isolated in streams fragmented by physical barriers such as dams or degraded habitats, or biotic barriers such as competition or hybridization with exotic salmonids. Recent conservation strategies were designed to safeguard populations from exotics by isolating cutthroat trout above impassable barriers. We examined the prognosis for long-term population persistence in stream fragments and the feasibility of the barrier approach by developing an analytical model to estimate the minimum stream lengths required by cutthroat trout of varying population densities and survivorship. Results calculated that over 4 km of stream was required to maintain an ending population size of 500 individuals at 40% survivorship with high fish densities and 20 km for low fish densities. Stream length required for 30% survivorship with N = 1000 was approximately 11 km for a population with high fish densities and over 54 km for streams with low fish densities. We regard the high fish density model estimates as absolute minimums because they were based on a stream-resident population inhabiting a well connected stream network containing ample food, habitat, and fish densities an order of magnitude higher than many extant populations. Our results suggest that many populations of cutthroat trout probably

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[3] Coauthored by Robert H. Hilderbrand and Jeffrey L. Kershner

cannot persist over the long term because of limited physical space. Similarly, barrier

construction for cutthroat trout conservation may be a necessary short-term solution, but a

long-term impediment. Successful conservation and restoration will require protection

from exotic species, the protection and formation of population core areas, and re-

establishment of population connectivity.

Introduction

Populations of cutthroat trout (*Oncorhynchus clarki*) have been in a state of decline

for many decades throughout the western United States. Behnke (1972) estimated that

99% of the original interior cutthroat trout populations have gone extinct within the last

100 years, and that only 2 of 13 subspecies of interior cutthroat trout stocks are stable or

increasing in number (Behnke 1992). Historical accounts indicate cutthroat trout were

once plentiful (reviewed in Trotter and Bisson 1988), but most subspecies now exist in

only small portions of their historical range. Westslope cutthroat trout (*O. c. lewisi*) exist

in only 11% of their historic range in Idaho and only 27% in Montana (McIntyre and

Rieman 1995), Colorado River cutthroat trout (*O. c. pleuriticus*) currently inhabit 1% of

their historic range (Behnke 1979), while Yellowstone cutthroat trout (*O. c. bouvieri*)

remain in 10% of their estimated original stream range of 24,000 km (Varley and

Gresswell 1988). Lahontan cutthroat trout (*O. c. henshawi*) inhabit 7% of their historic

stream range and 0.4% of lake areas (Gerstung 1988). Similarly, Bonneville cutthroat

trout (*O. c. utah*) currently occupy 5% of their native range (Kershner 1995) and were so

rare as to be reported extinct during the 1950's (Cope 1955).

Numerous reasons exist for the decline of interior cutthroat trout. The introduction of

non-native brook trout (*Salvelinus fontinalis*) typically results in range constriction or

elimination of cutthroat trout from streams (Moyle and Vondracek 1985; Varley and

Gresswell 1988). While rainbow trout (*O. mykiss*) and cutthroat trout coexist in west

coastal United States watersheds, interior cutthroat stocks evolved in allopatry and the

two species readily hybridize. This often results in the destruction of cutthroat trout

genotypes when rainbow trout are introduced (Behnke 1992; Bischoff 1995). Dam

construction on most small and large waterways has isolated migratory populations from

spawning and rearing tributaries (Thurow et al. 1988) and has probably resulted in the

loss of most fluvial populations. Water diversions and withdrawal for irrigation impede

trout recruitment through dewatering of spawning tributaries (Clancy 1988) and cause

isolation and population fragmentation. Exploitation by anglers has also contributed to

the decline in some populations (Thurow et al. 1988) where angling mortality can be high

because they are more easily caught by anglers than are other trout species (MacPhee

1966).

Recent management of cutthroat trout populations has been guide by a restrictive

paradigm that may actually endanger long-term population and subspecies persistence.

The common management prescription for cutthroat trout in the presence of exotic

species calls for population isolation above "impassable" barriers from potential threats

below. Martinez (1988, p. 88) recommended that "All remaining A populations [pure

Colorado River cutthroat trout] should be isolated by fish barriers to preclude

contamination with nonnative trouts." Similarly for Rio Grande cutthroat trout (*O. c.*

virginalis) conservation, "Nonnative salmonids will not be introduced into those portions

of streams occupied by Rio Grande cutthroat trout, and barriers will be constructed to

exclude nonnative salmonids from Rio Grande cutthroat trout habitats" (Stefferud 1988,

p. 91). Effective implementation results in a series of isolated populations that may still

be vulnerable to exotic invasions through human transplantation. The latest management

recommendations recognize the importance of population connectivity (van Eimeren

1996), but barriers remain popular.

The combination of climate, habitat degradation, exotic species, and barrier

construction has resulted in a series of population isolates distributed across the landscape

in fragments. Often these isolates are a headwater stretch of limited length. Of the 25

known populations of Bonneville cutthroat trout in southwestern Utah (6 remnant and 19

restored populations), the maximum available stream length was 16.4 km, with a median

of 4.5 km and a minimum of 1.4 km (Hepworth et al. 1997). Many of these populations

do not occupy all of the available stream so the estimates of available area are liberal.

Similar data are not readily available for other subspecies, but distribution maps presented

by Young et al. (1996) indicate that the vast majority of Colorado River cutthroat trout

populations exist in linear stream fragments (as opposed to multiple connected streams)

less than 20 km long.

    While sometimes implemented out of necessity, the barrier approach to cutthroat trout

conservation is widespread and creates demographic problems in extant populations that

have probably led to extinctions in other small isolates. The more spatially restricted a

population becomes, the greater the odds that a critical habitat component is insufficient

or missing for a life history stage, or that the absolute physical space necessary to

maintain a given population size no longer remains. Restricted range and spatial

autocorrelation (Hanski 1991) may intensify rather than spread the risks and effects of

perturbations such as droughts or floods. Population isolation may also reduce genetic

diversity through lack of gene flow and genetic drift (Lacy and Lindenmayer 1995;

Lindenmayer and Lacy 1995). When dealing with long-term persistence, it is probably

better to err on the side of caution and strive for as many breeding individuals as possible,

realizing that extinction risk increases as the number of individuals in a population

decreases.

    Limited physical space may not be a problem if individuals are sufficiently sedentary

so that they may be packed into a small area, but recent evidence indicates that

individuals in many trout populations move substantially more than formerly believed

(Young 1994; Brown and Mackay 1995; Gowan and Fausch 1996). Enhanced movement

not only means increased physical space required for population persistence, but also that

connectivity within and among critical habitats is crucial. The presence of barriers or

unhabitable stretches may result in substantial losses of individuals from the population

due to downstream movements. Additionally, isolated populations have increased

extinction risks (Fritz 1979; Smith 1980; Hanski 1986; Sjogren 1991) that can be alleviated with modest levels of immigration (Stacey and Taper 1992; Beier 1993). Small populations are often synonymous with limited space and are jeopardized through stochastic risks (Rieman and McIntyre 1993).

Much effort has been expended for cutthroat trout protection and restoration, but no information exists on the adequacy of stream fragment lengths for long-term population persistence. One approach is to estimate minimum stream length based on characteristics of a population having adequate resources and not confined in space. Such a population should behave as many populations probably did prior to current fragmentation levels, and would provide insights toward recovery. The Beaver Creek cutthroat trout population in southeast Idaho fulfills this. It is not fragmented, but consists of a network of 30+ km of inhabitable stream and probably represents how a "typical" stream-resident population should be comprised. Previous work has involved quantifying movements of cutthroat trout and potential competitive interactions with brook trout (Chapters 2 and 3). We use this information and new data to evaluate the efficacy of current cutthroat trout management techniques by estimating the minimum stream length (MSL) required by a cutthroat trout population for long-term persistence under differing effective population sizes and differing reach habitat types. Our objectives were to provide baseline estimates of required stream lengths, evaluate the current and future status of extant population isolates, and propose a general framework for restoration and reserve design in aquatic systems.

Methods

Study Area

Beaver Creek is a first-order stream originating at an altitude of 2400 m in southeast Idaho. It flows southerly for roughly 10 km before crossing into northern Utah and continues for another 9 km before joining the Logan River and eventually the Bear River, which empties into the Great Salt Lake. Beaver Creek makes up part of a continuous stream network of over 60 km (Fig. 4-1). The stream contains large, naturally reproducing populations of brook and cutthroat trout. Cutthroat trout predominate in higher gradient reaches, brook trout in beaver ponds, and the species transition in low gradient reaches. Beaver Creek also contains high aquatic invertebrate biomass and adequate food for trout.

Estimating MSL

We constructed a simple analytical model to estimate MSL based on a given ending population size, survivorship, and densities of adult and subadult fish within a given habitat type. The model took the form of $MSL = Ns^{-1}D^{-1}$ where N is the population size, s is the cohort survivorship, and D is the ambient trout density. We constructed MSL response curves for Beaver Creek, Idaho, and for an average Colorado River cutthroat trout population in the Uinta Mountains of Utah for population sizes of N=500, 750, 1000, 1500, and 2000 individuals with survivorship varying from 10-70%. Electrofishing catch data from Beaver Creek indicated that high gradient reach types contained an
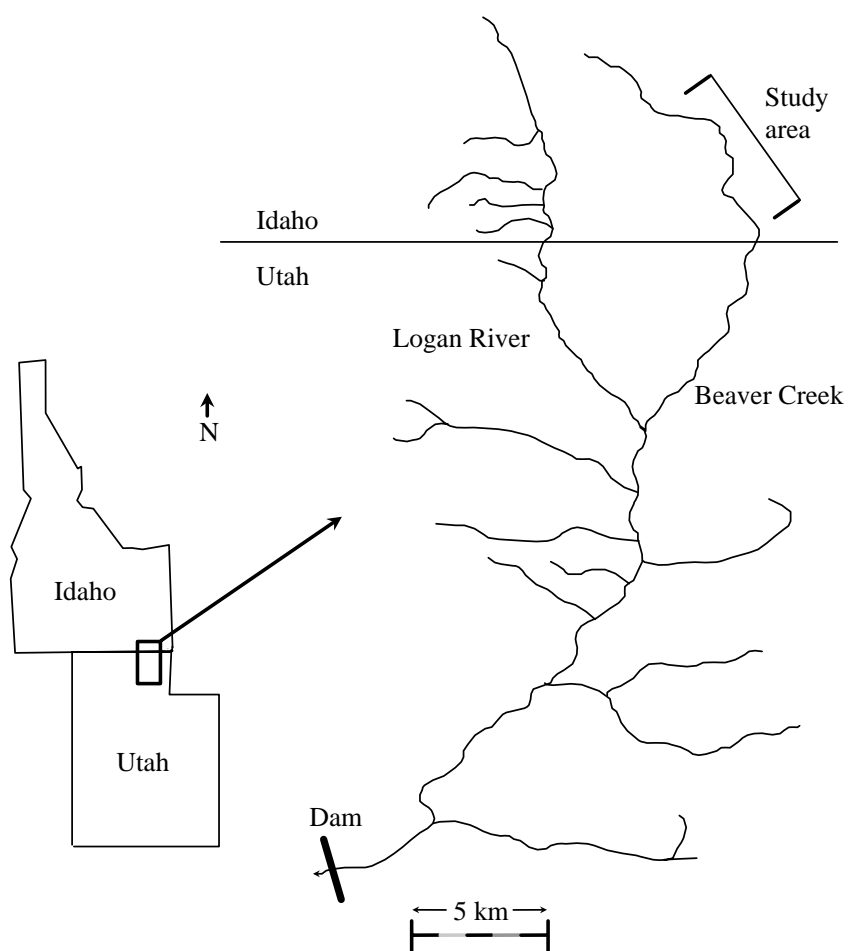
Figure 4-1. Location and network connectivity of Beaver Creek, Idaho-Utah.

average of 0.25 trout/m, low gradient reaches = 0.27 trout/m, and beaver ponds = 0.53

trout/m. We calculated a weighted ambient trout density for Beaver Creek, Idaho, of 0.31

trout/m based on a stream composed of 20% beaver ponds, 30% low gradient reaches,

and 50% high gradient reaches. For the Colorado River cutthroat trout population, we

used population estimates from Horan (1996), which resulted in 0.062 trout/m.

Results and Discussion

Evaluating critical needs for population persistence requires a multi-scale approach.

At the most basic level, the environment must fulfill a minimum set of life history

requirements allowing individuals to exist and reproduce. Failure to meet this minimum

set may result in a complete absence of individuals, a population sink requiring a source

for existence (Pulliam 1988), or migratory behaviors. Spatial connectivity among

habitats is crucial for persistence under these conditions. Areas meeting the minimum

life history requirements may still be constrained by food/space interactions (Chapman

1966) because salmonids form territorial hierarchies (Chapman 1966; Griffith 1972;

Grant et al. 1989) so that a minimum viable population size cannot be achieved in the

available space. Finally, the sociopolitical arena, the amount and arrangement of

physical space, the juxtaposition of populations, and connectivity between populations

determine the potential for long-term persistence in an ever-changing landscape.

Comparing MSL estimates with stream lengths of extant cutthroat trout populations

indicates that many could be in danger. The only known published paper with cutthroat

trout survivorship gives approximate values of 40% (Miller 1953) when factored through time. For an ending population size of 500 with 40% survivorship, the Beaver Creek population requires at least 4 km of stream and the Uinta populations at least 20 km (Fig. 4-2). The data from Hepworth et al. (1997) indicate 9 of the 15 established populations of Bonneville cutthroat trout in southwestern Utah currently inhabit 4 km of stream or less, and 5 of the 15 have total available stream lengths less than 4 km. Considering all of their populations (including those recently introduced and having limited ranges), only 11 of 25 populations inhabit streams with available total lengths over 4 km. We must exercise caution in these interpretations because the relative productivity of the streams sampled by Hepworth et al. (1997) is not known. Increased food availability may override space interactions and allow higher fish densities per unit stream length and less stream required for population viability. Fish densities reported in Hepworth et al. (1997) are comparable to those in Beaver Creek, ranging 0.118-0.546 trout/m and an average density (0.22 trout/m) approximately 30% below Beaver Creek, but still an order of magnitude greater than the Uinta populations.

The assumption of 500 individuals ensuring long-term persistence is overly optimistic.   Female westslope cutthroat trout do not breed until 140 mm in length (Downs et al. 1997), but MSL estimates were based on individuals > 120 mm. Most females in Downs et al. (1997) were at least 4 years old at the time of first breeding. If this is true of most stream-resident cutthroat trout populations, survivorship is probably somewhere between 20-40% and we should plan more conservatively to account for
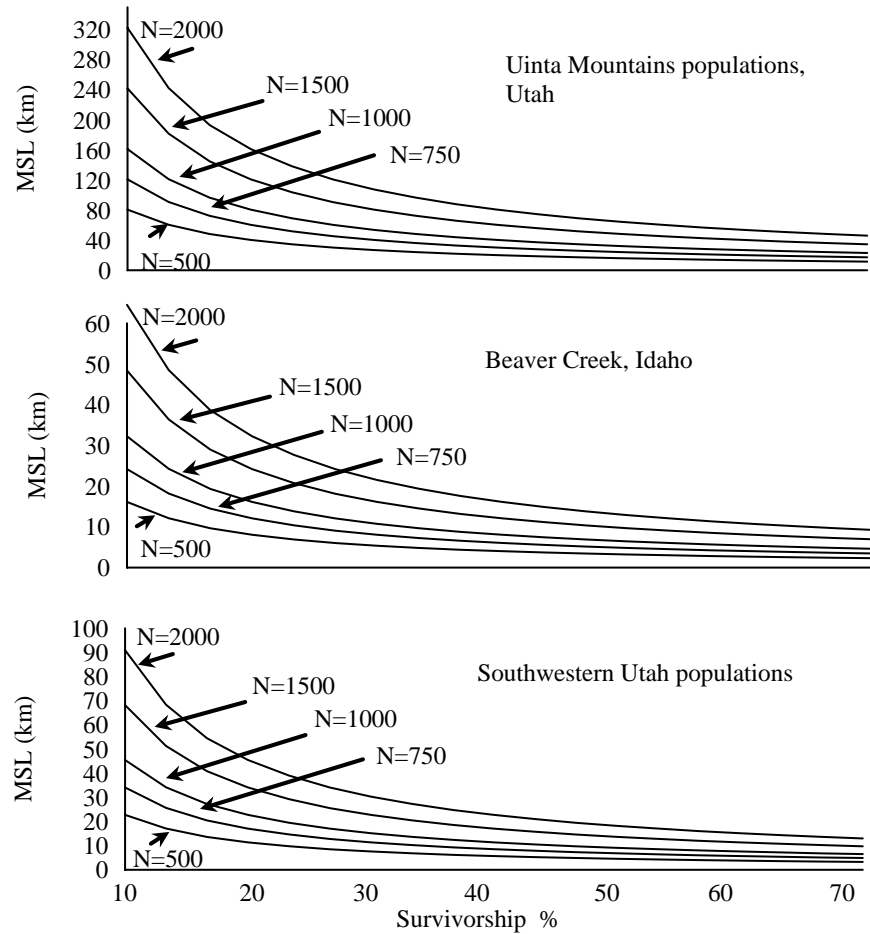
Figure 4-2. Minimum stream length curves for population sizes of 500, 750, 1000, 1500,

and 2000 individuals for varying levels of cohort survivorship for Colorado River

cutthroat trout in the Uinta Mountains (top), Utah, for Beaver Creek, Idaho (center), and

for southwestern Utah populations (bottom using data from Hepworth et al. (1997). Note

different values on Y-axis.

consecutive years of poor survival. We might therefore use a survivorship of 20% to account for rare events. This would increase MSL for the Beaver Creek population to 8 km at 500 individuals and 40 km for the Uinta populations (Fig. 4-2). Additionally, the effective population size is often an order of magnitude lower than the actual population size (Frankham 1995). If true, then 500 adults and subadults are probably not sufficient to maintain genetic diversity over a period of decades or centuries, especially if populations are isolated with no gene exchange.

Increasing the minimum viable population size for long-term persistence to a more realistic value of 1000 individuals places most populations in serious jeopardy of insufficient space. The MSL required at a 30% survivorship is approximately 11 km for the Beaver Creek population and 54 km for the Uinta populations (Fig. 4-2). Under this scenario, only three of the populations listed in Hepworth et al. (1997) inhabit streams with sufficient space under the high fish density scenario, and none of these populations have expanded to beyond 5 km. Similarly, the majority of Colorado River cutthroat trout populations (shown in Young et al. 1996) could not persist.

Our results based on the Beaver Creek population represent a best-case scenario and probably reflect the absolute minimum stream required. Food and habitat did not appear to be limiting, and MSL estimates were based on a static fish distribution, or, if movements occurred, individuals merely exchanged places. Movements in Beaver Creek were generally less than 1 km (Chapter 2) and we cannot predict how fish densities would change in relation to movements. Other investigators have reported annual movements

on the order of tens of kilometers for trout in larger stream systems still sufficiently connected (Bjornn and Mallet 1964; Clapp et al. 1990; Meyers et al. 1992; Young 1994). Movements of this magnitude might drastically increase MSL, or the mobile population fraction would exit the population as mortality when in the presence of barriers or small fragments.

We can construct a conceptual model (Fig. 4-3) based on the literature to predict the relative space requirements of a given population size due to changes in food amount or quality and habitat conditions. High levels of food and habitat result in less space for a given number of individuals. Decreasing one or both of these components decreases the values on the axes, resulting in greater stream length required. Chapman (1966) hypothesized that food and the degree of visual isolation regulated population density because most stream-dwelling salmonids establish territories (Jenkins 1969; Dill et al. 1981; McNicol and Noakes 1981; McNicol et al. 1985; Grant et al. 1989; Grant 1990; Grant and Kramer 1990; Keeley and Grant 1995). Increasing food supply can decrease aggressiveness or the area of territory defended (Symons 1971; Slaney and Northcote 1974) and allow higher densities. The degree of visual isolation or complexity is usually defined in terms of the diversity or abundance of habitat types and structural elements such as logs, rocks, or overhead cover that fish can use as cover (Bisson et al. 1987; Sullivan et al. 1987; Pearsons et al. 1992; Reeves et al. 1993). Increased complexity can provide habitat and refugia from disturbance (Sedell et al. 1990), reduce predation risk (McMahon and Hartman 1989), increase population stability and community resistance to

disturbance (Pearsons et al. 1992), and increase species diversity (Reeves et al. 1993).

Increased complexity or cover often results in greater abundances of trout and salmon

(Hunt 1969; Lewis 1969; House and Boehne 1985, 1986; Wesche et al. 1987; Moore and

Gregory 1988; McMahon and Hartman 1989; Riley and Fausch 1995). These factors

probably exhibit an inverse relationship with space required for a population; less food or

simplified habitats should require more stream to maintain a given population size.

The conceptual model is overly simplistic in the current form, but each axis can be

expanded to include other variables. The axis relationships also change among the reach

habitat types because of changes in water velocities, cover elements, food availability,

and the predominance of brook trout in beaver ponds and lower gradients and cutthroat

trout in higher gradients. Each aspect may be parameterized to build a predictive MSL

model with management value for identifying populations at risk and streams possessing

a high probability for successful reintroductions of cutthroat trout. Unfortunately,

construction of an adequate predictive model was beyond our data. Our MSL estimates

were based on a saturated model using all available density relationships, but should still

provide a sufficient baseline for comparison.

The presence of brook trout may decrease either axis of the conceptual model (Fig. 4-

3). If the mechanism of cutthroat trout exclusion by brook trout is exploitative

competition, then brook trout would reduce values on the food axis. Similarly, if the

mechanism is interference competition, brook trout would enter the model on the habitat

axis. The presence of brook trout could substantially lower cutthroat trout densities and
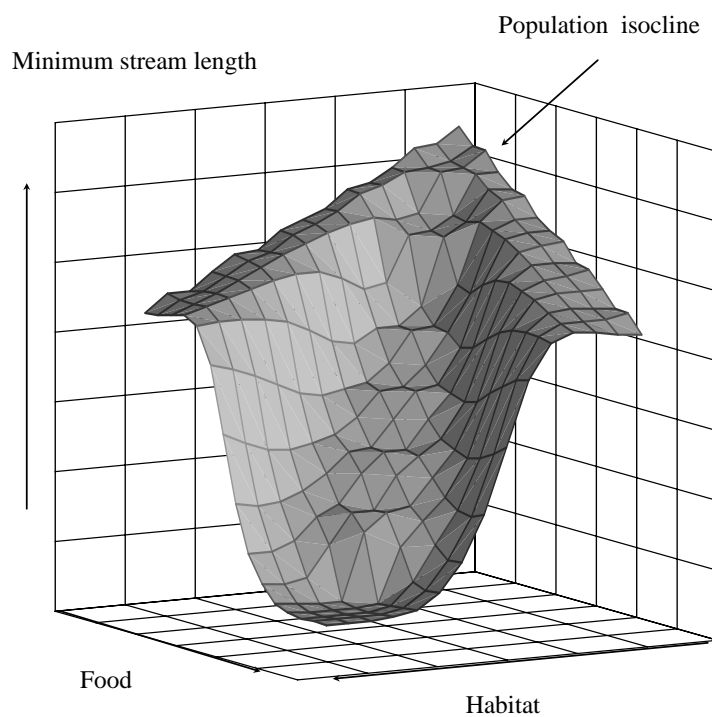
Figure 4-3. A conceptual relationship between food, habitat, and the length of stream required to maintain a given population density.

increase stream length required. Of those Colorado River cutthroat trout populations not yet eliminated by brook trout, nearly half have been invaded (Young et al. 1996). Invasion rates by brook trout are not known for the other cutthroat trout subspecies' populations, but they remain a potential threat. Regardless of the mechanism of exclusion, the presence of brook trout will greatly expand stream length requirements and could render many low velocity habitat reaches unsuitable for cutthroat trout (Griffith 1972; Chapter 3).

Insufficient space for long-term persistence does not mean populations cannot thrive for long periods. Populations may be deterministically declining, but the high variability inherent in salmonid populations (Platts and Nelson 1988) may mask downward trends for many years. However, the existence of nearby populations could function as a metapopulation (Levins 1969; Rieman and McIntyre 1993) where small amounts of immigration may allow persistence (Stacey and Taper 1992) even if all populations are fragments. Documentation of metapopulation structure and function in salmonids does not exist, but long movements and seasonal migrations in connected systems (e.g., Bjornn and Mallet 1964; Bernard and Israelsen 1982; Young 1994; Brown and Mackay 1995) imply the potential.

The current state of cutthroat trout population isolates requires active restoration efforts if any of the various subspecies are to persist. The first efforts should focus on protecting those populations inhabiting the longest and most well connected networks. Focusing first on the strongest populations while ignoring those more at risk may appear

counterintuitive, but the largest populations should be ensured adequate space before expanding efforts. Focusing exclusively on the smallest populations and assuming that the largest are sufficient could result in all populations in a basin deterministically declining.

Protection of the largest cores must occur at the watershed level because streams are catchments controlled by all impacts and processes upslope and bear those cumulative effects. Biotic as well as physical protection must be afforded. This means that exotic species such as brook, brown, and rainbow trout must be controlled through removal by electrofishing or toxicants. Although it may appear unrealistic to remove all such biotic threats, expecting cutthroat trout populations isolated above barriers to persist indefinitely is equally unrealistic. Because most isolates are restricted to headwater reaches, the populations are locally clumped. Large-scale disturbances like the Yellowstone wildfires or severe droughts could readily eliminate all populations in multiple basins or even an entire subspecies. This nearly happened to the Gila trout (*O. gilae*; Propst et al. 1992) and could easily happen again. We must remember that streams within watersheds are not static and that periodic disturbances probably rendered some streams or entire watersheds uninhabitable for years or decades (Reeves et al. 1995), but that connectivity between systems allowed recolonization of perturbed systems by population cores.

Once the population cores are sufficiently protected, efforts should be expanded to the smaller fragments. Until adequate predictive models are developed, our MSL estimates can be applied to evaluate those populations most at risk, those most likely to benefit

from modest efforts, and candidate streams for population reintroductions. By using core areas as anchors, efforts may be directed toward linking fragments to cores (Rieman and McIntyre 1993; Fig. 4-4) or to establishing new populations in proximity to core areas. Once enough populations are established within a drainage to safeguard against short-term extinction, restoration efforts could be further expanded to reintroductions into historic ranges not currently occupied. In short, we advocate establishing foundations and building outward rather than starting diffusely and hoping for consolidation. Many of the strongest populations currently reside in wilderness or roadless areas (Gresswell 1995; McIntyre and Rieman 1995; Kershner et al. 1997).

Some stream fragments may never provide enough space to sustain long-term viable populations despite natural reproduction. These island populations (Harrison 1991) have and will continue to rely on immigration from a mainland or population core. In this case, rather than focus on restoring stream sections contiguous with existing populations, a better conservation approach might involve restoring currently uninhabited stream sections in-between populations (Fig. 4-4). These sections could serve as stopover areas for immigrants between populations and might also house small populations themselves. This further increases the importance of restoring and maintaining population cores.

Optimal reserve design structure is still unknown for stream systems. Streams are complicated by their reduced dimensionality; although streams are three-dimensional and move across the landscape in two-dimensional space, their linearity forces aquatic

Population isolate
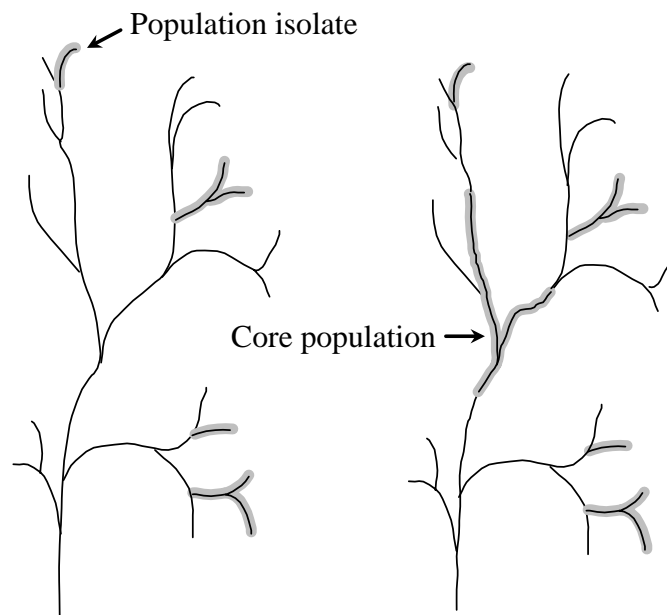
Core population →

Figure 4-4. An example of how core areas and increased connectivity could alleviate

effects of population isolation and aid in restoration and persistence.

organisms into following a one-dimensional pathway for immigration. However, parallels from terrestrial reserve design can still be drawn. For example, for a given length or area, is it better to have one long stream segment or a network of connected streams? Branched networks spread the risk from catastrophes, but would most likely be composed of smaller water volumes, narrower channels, and shallower habitats not capable of holding as many individuals as would the same amount of stream in a linear segment. However, branched networks would probably contain a greater diversity of habitat types and food sources and could provide a greater variety of alternate choices for populations to cope with changing environmental conditions. Additionally, the branched network approach probably traverses greater landscape area and geomorphology, thus reducing spatial autocorrelation in environmental variables.

Configuration of stream reserves will probably depend on the political arena, the disturbance regime and forms, and on the landscape itself. All decisions will be tightly constrained by lawmakers, the public, and the local economy. After sociopolitical forces determine the subset of watersheds actually available for protection and restoration, current and potential cutthroat trout populations should be identified and depicted in a spatial context. The demographically strongest populations and those inhabiting areas with the most available habitat should become the focus of efforts to establish population cores. The configuration of conservation areas for range expansions and population isolates should be contingent on available stream length or area. Providing this condition is fulfilled, the actual configuration will depend on local and regional disturbance

regimes. Populations in areas with frequent disturbances should be arranged in networks to spread the risk and provide refugia and recolonization areas. Populations in regions with infrequent disturbances may benefit from linear segments containing higher quality habitats than headwater streams, especially if headwater streams experience harsher climatic conditions than larger segments.

The ensured long-term persistence of cutthroat trout in the interior western United States requires a consolidated, hierarchical approach. Assuming all life history requirements are met, large continuous stream segments are still required for population longevity. The isolation of cutthroat trout populations above barriers may be necessary for short-term survival against invasions of exotic salmonids. However, most of these population isolates do not possess adequate physical space for long-term persistence. It is critical to eliminate biotic threats and establish population core areas from which dispersal through restored segments will maintain the genetic and demographic integrity of fragments until further conservation and restoration can reestablish natural networks.

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CHAPTER 5

CONCLUSION

The ensured persistence of cutthroat trout depends on a number of factors of which only a few are addressed in this research. Conservation must be approached within a hierarchical framework that includes not only life history characteristics and abundance at small spatio-temporal scales, but also through interspecific interactions and stream reach characteristics at moderate scales, and landscape-level features such as underlying geology governing stream productivity, realized and potential connectivity with other streams, the juxtaposition of other viable populations and the degree of isolation, and the recurrence intervals of catastrophic disturbances. Concentrating on only one scale while ignoring the others will ultimately limit our ability to understand and manage populations and the species.

The results of my research have shown that salmonids move much more than previously thought. Similar growth rates between the mobile and sedentary population components indicate that they are alternative strategies and that mobile fish in Beaver Creek are not inferior in some way, but are an important, newly recognized dimension to fish populations. The mobile population fraction is probably a hedge against catastrophic disturbance and a way to expand ranges and exchange genes with other populations. We must ensure that sufficient stream length exists to maintain this component for long-term adaptation and survival.

Similar growth rates among the three predominant reach habitat types in Beaver Creek, high gradient, low gradient, and beaver ponds, imply that cutthroat trout are well suited for living in all areas, but attain their highest localized densities in beaver ponds. Less stream is theoretically required for population persistence when beaver ponds are present, but this type of habitat is transient and contains the highest densities of brook trout.

Although adult cutthroat trout appear competitively equal with brook trout when cutthroat are the first to establish residence, brook trout may cause habitat shifts which exclude cutthroat when individuals of the two species simultaneously invade an area or if brook trout are already established. Rarely do adult cutthroat trout successfully establish in areas already occupied by conspecifics or brook trout. My findings coupled with the knowledge that brook trout are well suited to low-velocity environments like beaver ponds could help to explain the elimination of cutthroat trout from most streams where brook trout have been introduced. However, the results do not rule out species replacement occurring in other size classes of trout not studied. Competitive exclusion could occur in the very young life history stages not examined in the current research. This avenue warrants further examination.

In light of cutthroat trout movement patterns, reach-specific densities, and numerical dominance of beaver ponds by brook trout, it is critical to provide more space than is currently available to most extant populations. The barrier and isolation approach to cutthroat trout conservation will probably result in the eventual extirpation of cutthroat

trout and further range expansions of exotic salmonids. Effective conservation and

restoration depends on elimination of exotics, provision of sufficient stream length or

area, and restored connections between isolated populations.

APPENDICES

Appendix A.

ANCOVA Tables

Table A-1. ANCOVA examining growth between sedentary and mobile cutthroat trout with fish length as a covariate.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	0.00315565	0.00105188	0.28	0.8358
Error	22	0.08125501	0.00369341		
Corrected Total	25	0.08441066			

R-Square	C.V.	Root MSE	Mean
0.037384	74.46596	0.06077343	0.08161236

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Growth	1	0.00250725	0.00250725	0.68	0.4188
Length	1	0.00034754	0.00034754	0.09	0.7619
Growth*Length	1	0.00223450	0.00223450	0.60	0.4450

Table A-2. ANCOVA examining growth among habitat types for sedentary cutthroat trout with fish length as a covariate.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	0.01214188	0.00242838	0.79	0.5935
Error	6	0.01846325	0.00307721		
Corrected Total	11	0.03060512			

R-Square	C.V.	Root MSE	Mean
0.396727	82.88873	0.05547259	0.06692416

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Growth	2	0.00477233	0.00238617	0.78	0.5017
Length	1	0.00008952	0.00008952	0.03	0.8702
Growth*Length	2	0.00656119	0.00328059	1.07	0.4016

Table A-3. ANCOVA examining growth among habitat types for mobile cutthroat trout with fish length as a covariate.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	0.02647490	0.00529498	5.18	0.1030
Error	3	0.00306405	0.00102135		
Corrected Total	8	0.02953895			

R-Square	C.V.	Root MSE	Mean
0.896271	45.23735	0.03195856	0.07064639

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Growth	2	0.01009247	0.00504623	4.94	0.1124
Length	1	0.00363585	0.00363585	3.56	0.1557
Growth*Length	2	0.01413713	0.00706856	6.92	0.0752

Table A-4. ANCOVA examining growth between brook trout and cutthroat trout with fish length as a covariate.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	0.01209747	0.00403249	1.10	0.3646
Error	27	0.09860528	0.00365204		
Corrected Total	30	0.11070275			

R-Square	C.V.	Root MSE	Mean
0.109279	68.17194	0.06043217	0.08864670

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Growth	1	0.00081812	0.00081812	0.22	0.6398
Length	1	0.00412084	0.00412084	1.13	0.2975
Growth*Length	1	0.00230690	0.00230690	0.63	0.4337

Appendix B.

ANOVA Tables

Table B-1. ANOVA examining abundance of drifting invertebrates among habitat types.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	0.43456976	0.21728488	0.45	0.6594
Error	6	2.91789107	0.48631517		
Corrected Total	8	3.35246082			

R-Square	C.V.	Root MSE	Mean		
0.129627	22.62738	0.69736301	3.08194343		

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Habitat	2	0.43456976	0.21728488	0.45	0.6594

Table B-2. ANOVA comparing the effect of brook trout versus cutthroat trout added as competitors on threshold density of the radio-tagged resident cutthroat trout.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	11.25653595	11.25653595	2.81	0.1036
Error	32	128.36111111	4.01128472		
Corrected Total	33	139.61764706			

R-Square	C.V.	Root MSE	Mean
0.080624	42.03448	2.00281919	4.76470588

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Species	1	11.25653595	11.25653595	2.81	0.1036

Table B-3. ANOVA comparing the effect of habitat type on threshold density of the radio-tagged resident cutthroat trout.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	1.43393494	0.71696747	0.16	0.8521
Error	31	138.18371212	4.45753910		
Corrected Total	33	139.61764706			

R-Square	C.V.	Root MSE	Mean
0.010270	44.31099	2.11128849	4.76470588

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Habitat	2	1.43393494	0.71696747	0.16	0.8521

Table B-4. ANOVA comparing the effect of brook trout versus cutthroat trout added as competitors on threshold density of the radio-tagged resident cutthroat trout in high-gradient-reach habitat types.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	16.59393939	16.59393939	2.68	0.1358
Error	9	55.63333333	6.18148148		
Corrected Total	10	72.22727273			

R-Square	C.V.	Root MSE	Mean
0.229746	49.27720	2.48625853	5.04545455

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Habitat	1	16.59393939	16.59393939	2.68	0.1358

Table B-5. ANOVA comparing the effect of brook trout versus cutthroat trout added as competitors on threshold density of the radio-tagged resident cutthroat trout in low-gradient-reach habitat types.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.85227273	0.85227273	0.29	0.6028
Error	9	26.37500000	2.93055555		
Corrected Total	10	27.22727273			

R-Square	C.V.	Root MSE	Mean
0.031302	37.66150	1.71188654	4.54545455

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Habitat	1	0.85227273	0.85227273	0.29	0.6028

Table B-6. ANOVA comparing the effect of brook trout versus cutthroat trout added as competitors on threshold density of the radio-tagged resident cutthroat trout in beaver pond habitat types.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.37202381	0.37202381	0.10	0.7619
Error	10	38.35714286	3.835714286		
Corrected Total	11	38.72916667			

R-Square	C.V.	Root MSE	Mean
0.009606	41.59642	1.95849796	4.70833333

Source	DF	ANOVA SS	Mean Square	F Value	Pr > F
Habitat	1	0.37202381	0.37202381	0.10	0.7619

Appendix C.

Habitat Measurements for Experimental Sections
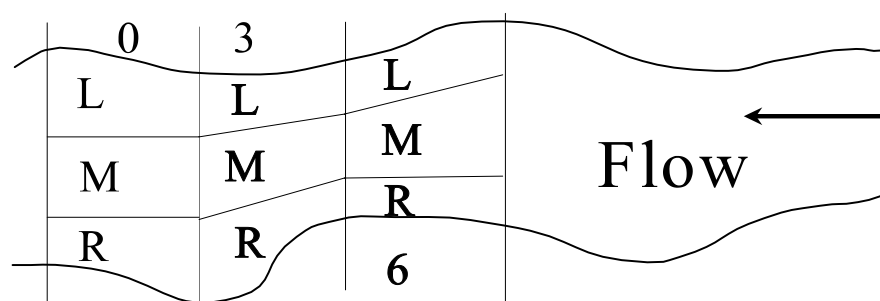
Fig. C-1. A schematic of where habitat measures were taken for the experimental stream sections in the competitor addition experiments (1996) and displacement experiments (1997). Numbers indicate the distance from the bottom of the section in 3-m increments while letters indicate position within the stream: L = left margin, M = midchannel, R = right margin. For substrate measures: s gravel = small gravel; l gravel = large gravel

Table C-1. Habitat measurements for each cell in section 1 (high gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.06	15.7	S gravel	3	0	40	10	40	0	0
0	2	slow	1.17	24.7	S gravel	1	0	45	25	50	0	0
0	3	slow	1.19	27.5	S gravel	2	0	40	20	49	0	0
3	1	slow	1.21	14.5	Cobble	3	2	45	15	45	0	0
3	2	medium	1.06	18.9	Cobble	7	0	30	0	40	0	0
3	3	medium	1.16	19.5	S gravel	2	0	25	15	30	0	1
6	1	slow	1.27	10.8	L gravel	6	0	30	0	40	0	0
6	2	medium	1.33	16.5	L gravel	3	0	30	5	50	0	0
6	3	medium	1.26	14.9	S gravel	5	0	20	5	35	0	0
9	1	slow	1.06	11.6	L gravel	3	0	20	5	30	0	0
9	2	fast	1.15	14.3	Cobble	6	0	20	0	25	0	0
9	3	fast	1.17	18.6	Cobble	3	0	25	0	40	0	0
12	1	fast	1.07	10.7	Cobble	1	1	20	5	30	0	0
12	2	fast	1.19	18.3	Cobble	1	0	30	0	30	0	0
12	3	fast	1.33	15.6	Cobble	1	0	20	0	25	0	0
15	1	fast	1.18	12.7	Cobble	1	0	25	0	35	0	0
15	2	fast	1.14	11.2	Boulder	0	0	15	5	20	0	0
15	3	fast	1.24	14.9	Boulder	0	0	20	5	30	0	0
18	1	medium	1.25	8.7	Cobble	2	0	30	10	30	0	1
18	2	medium	1.20	15.1	Cobble	1	0	30	5	35	0	0
18	3	medium	1.45	17.9	Cobble	3	0	30	10	40	0	0
21	1	fast	1.27	9.1	S gravel	0	0	20	10	25	0	1
21	2	medium	1.27	15.8	Cobble	2	0	30	5	40	0	0
21	3	slow	1.31	19.2	Cobble	4	0	30	5	35	0	1
24	1	slow	1.13	7.1	S gravel	0	1	10	0	10	0	0
24	2	fast	1.20	16.2	Cobble	5	0	25	0	30	0	0
24	3	fast	1.40	15.3	Boulder	2	1	20	0	30	0	1

Table C-2. Habitat measurements for each cell in section 2 (high gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.05	12.3	S gravel	1	1	20	10	40	0	0
0	2	medium	1.27	20.7	Cobble	5	0	30	0	40	0	0
0	3	slow	1.27	16.7	S gravel	0	1	20	10	30	0	0
3	1	slow	1.47	14.5	Boulder	1	1	40	20	40	0	0
3	2	medium	1.22	16.5	Cobble	4	1	25	0	30	0	0
3	3	medium	1.23	15.9	S gravel	1	1	20	5	30	0	0
6	1	slow	1.14	12.5	S gravel	1	1	30	20	40	1	0
6	2	medium	1.23	18.3	Boulder	5	0	30	20	40	0	0
6	3	slow	1.30	18.4	L gravel	1	1	25	20	30	0	0
9	1	slow	1.36	10.1	S gravel	2	1	25	10	40	1	0
9	2	medium	1.54	20.6	Boulder	4	4	40	10	50	0	0
9	3	medium	1.48	17.9	Cobble	4	2	25	5	30	0	0
12	1	medium	1.29	11.5	Boulder	3	0	25	0	35	1	0
12	2	medium	1.28	20.9	Boulder	6	0	40	0	45	0	0
12	3	medium	1.27	15.4	S gravel	2	0	20	5	30	0	0
15	1	medium	1.29	11.5	Boulder	3	0	25	0	35	1	0
15	2	medium	1.28	20.9	Boulder	6	0	40	0	45	0	0
15	3	medium	1.27	15.4	S gravel	2	0	20	5	30	0	0

Table C-3. Habitat measurements for each cell in section 3 (high gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.35	16.4	Boulder	5	2	45	10	50	0	0
0	2	slow	1.42	23.1	Boulder	9	1	40	0	50	0	0
0	3	slow	1.50	23.7	Cobble	2	0	35	15	45	1	0
3	1	slow	1.04	17.5	Cobble	5	0	35	0	50	1	0
3	2	slow	1.21	27.9	Cobble	6	0	45	0	45	0	0
3	3	slow	1.21	23.1	S gravel	2	1	30	20	35	1	0
6	1	slow	1.35	13.9	S gravel	3	0	30	25	40	1	0
6	2	medium	1.54	21.6	Cobble	4	0	35	0	40	0	0
6	3	slow	1.59	22.2	S gravel	1	2	30	10	30	0	0
9	1	fast	1.46	9.9	Boulder	1	0	20	0	30	0	0
9	2	fast	1.18	17.6	Boulder	0	0	30	0	40	0	0
9	3	fast	1.41	18.4	Boulder	2	3	25	0	30	0	0
12	1	medium	1.10	11.1	L gravel	1	0	40	10	40	0	0
12	2	fast	1.32	16.8	Boulder	2	0	30	5	50	0	0
12	3	medium	1.51	19.2	S gravel	0	0	30	10	40	0	0
15	1	medium	1.75	8.7	Boulder	0	1	30	5	40	0	0
15	2	fast	1.71	13.9	Boulder	0	0	30	10	50	0	0
15	3	fast	1.81	15.3	Boulder	0	0	25	20	35	0	0
18	1	medium	1.16	11.4	Boulder	2	0	30	10	40	0	0
18	2	fast	1.32	14.7	Boulder	0	0	30	20	40	0	0
18	3	fast	1.50	16.9	Boulder	1	0	25	10	30	0	0
21	1	fast	1.90	9.5	Boulder	0	1	25	10	35	0	0
21	2	fast	1.60	13.7	Boulder	0	0	25	10	35	0	0
21	3	fast	1.32	17.5	Boulder	0	0	25	10	35	0	0
24	1	fast	1.86	7.5	Boulder	0	1	25	10	35	0	0
24	2	fast	1.53	14.9	Boulder	0	0	35	10	35	0	0
24	3	medium	1.52	16.8	Cobble	0	0	30	10	40	0	0
27	1	medium	1.67	8.9	L gravel	0	0	25	10	30	0	0
27	2	medium	1.44	15.4	Boulder	1	0	35	10	40	0	0
27	3	slow	1.46	14.8	Silt	1	1	25	20	30	0	0
30	1	fast	1.15	6.6	Boulder	0	0	10	5	20	0	0
30	2	medium	1.16	16.8	Boulder	2	0	30	0	40	0	0
30	3	fast	1.23	22.1	Cobble	0	1	35	20	40	0	0

Table C-4. Habitat measurements for each cell in section 4 (low gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.27	10.8	Silt	0	0	30	30	30	0	0
0	2	slow	1.19	18.9	Silt	0	0	35	35	40	0	0
0	3	slow	1.20	19.2	Silt	0	0	30	30	30	0	0
3	1	slow	1.70	9.5	Silt	0	0	25	20	30	1	0
3	2	slow	1.32	19.2	L gravel	0	0	45	30	60	0	0
3	3	slow	1.41	25.4	L gravel	0	0	50	40	65	1	0
6	1	slow	1.45	11.8	Silt	0	0	40	25	55	1	0
6	2	slow	1.33	23.4	L gravel	0	0	65	60	75	0	0
6	3	slow	1.35	20.9	Silt	0	0	35	35	40	1	1
9	1	slow	1.44	9.9	S gravel	0	0	35	30	40	0	0
9	2	slow	1.00	21.6	Cobble	1	0	50	40	65	0	0
9	3	slow	1.30	20.6	Silt	0	0	35	30	35	0	1
12	1	slow	1.17	12.1	S gravel	0	0	35	30	40	0	0
12	2	slow	1.14	19.5	Boulder	1	0	50	40	60	0	0
12	3	medium	1.20	19.2	L gravel	1	0	30	25	30	0	1
15	1	slow	1.40	11.1	S gravel	0	0	40	30	50	0	0
15	2	slow	1.33	17.7	Cobble	3	0	50	25	60	0	0
15	3	slow	1.34	20.9	Boulder	2	0	40	0	55	0	1
18	1	slow	1.67	13.4	S gravel	0	0	50	40	60	1	0
18	2	slow	1.03	25.4	Cobble	0	0	60	55	70	0	0
18	3	slow	1.32	24.4	Cobble	1	0	40	20	40	0	0
21	1	slow	1.06	17.7	L gravel	0	0	65	65	65	0	0
21	2	slow	1.09	25.8	Boulder	0	0	55	50	65	0	0
21	3	slow	1.10	26.4	Silt	0	0	40	30	50	0	0
24	1	slow	1.89	10.8	Cobble	1	0	50	40	70	1	1
24	2	slow	1.22	25.2	L gravel	1	0	65	65	70	0	0
24	3	slow	1.25	26.6	Silt	0	0	40	30	45	0	0
27	1	slow	1.45	12.2	Cobble	0	1	45	30	60	1	1
27	2	slow	1.35	19.6	Cobble	1	0	55	50	65	0	0
27	3	slow	1.47	19.7	Silt	0	0	30	20	50	0	0
30	1	slow	1.78	11.3	Cobble	0	0	65	50	75	0	0
30	2	slow	1.42	17.6	Cobble	0	0	45	40	50	0	0
30	3	slow	1.31	17.9	S gravel	0	0	30	25	40	0	0
33	1	slow	1.45	12.2	Silt	0	0	45	30	60	0	0
33	2	slow	1.21	31.7	Silt	0	0	70	60	75	0	0
33	3	slow	1.14	32.1	S gravel	0	0	50	30	70	0	0
36	1	medium	1.21	14.9	S gravel	0	0	50	40	65	0	0
36	2	slow	1.11	26.5	S gravel	0	0	50	40	70	0	0
36	3	medium	1.15	24.3	S gravel	0	0	35	30	50	0	0

Table C-5. Habitat measurements for each cell in section 5 (low gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.88	8.7	S gravel	0	0	30	30	35	0	0
0	2	slow	1.33	17.8	S gravel	0	0	40	35	40	0	0
0	3	slow	1.40	21.3	S gravel	0	0	40	35	40	1	0
3	1	slow	1.27	11.3	S gravel	0	0	35	30	40	0	0
3	2	slow	1.18	19.2	S gravel	0	0	35	30	40	0	0
3	3	slow	1.24	23.4	S gravel	0	1	40	35	40	1	0
6	1	slow	1.30	20.2	S gravel	0	0	60	60	65	1	0
6	2	slow	1.13	26.9	S gravel	0	1	60	55	65	0	0
6	3	slow	1.33	28.9	S gravel	0	1	55	50	60	1	0
9	1	slow	1.22	10.2	S gravel	0	0	40	40	55	1	0
9	2	slow	1.18	18.1	L gravel	0	0	60	50	70	0	0
9	3	slow	1.52	20.9	S gravel	0	0	60	50	70	1	0
12	1	slow	1.10	10.1	S gravel	0	0	30	25	40	0	0
12	2	slow	1.04	23.3	L gravel	0	0	60	50	60	0	0
12	3	slow	1.09	24.4	Silt	0	0	45	40	60	1	0
15	1	slow	1.57	8.2	S gravel	0	0	35	25	40	0	0
15	2	slow	1.62	23.9	Boulder	2	0	60	55	60	0	0
15	3	slow	1.57	17.3	Silt	1	0	25	20	40	0	0
18	1	slow	1.83	7.2	S gravel	0	0	35	30	40	0	0
18	2	slow	1.36	20.8	Cobble	3	0	55	50	60	0	0
18	3	slow	1.26	19.2	Cobble	2	1	30	25	40	0	0
21	1	slow	1.57	8.6	S gravel	0	0	45	30	50	0	0
21	2	slow	1.22	21.4	Cobble	0	0	55	50	60	0	0
21	3	slow	1.25	23.1	Boulder	1	0	40	30	45	0	0
24	1	slow	1.00	17.6	S gravel	0	0	55	50	60	0	0
24	2	slow	1.28	26.3	S gravel	0	0	65	60	65	0	0
24	3	slow	1.22	23.3	Cobble	2	0	35	25	50	0	0
27	1	slow	1.50	15.4	S gravel	0	0	55	55	60	0	0
27	2	slow	1.29	24.1	S gravel	0	0	55	50	65	0	0
27	3	slow	1.20	29.1	Silt	0	1	45	40	60	0	0
30	1	slow	1.62	14.6	S gravel	0	0	55	55	60	0	0
30	2	slow	1.16	30.2	S gravel	0	0	65	60	65	0	0
30	3	slow	1.26	30.2	Silt	0	0	50	45	60	0	0
33	1	slow	1.27	12.8	S gravel	0	0	55	50	60	1	0
33	2	slow	1.07	25.2	S gravel	0	0	65	60	70	0	0
33	3	slow	1.19	29.7	Silt	0	0	50	40	60	0	0
36	1	medium	1.24	17.1	S gravel	0	0	50	40	55	1	0
36	2	slow	1.22	21.5	S gravel	0	0	45	35	60	0	0
36	3	slow	1.17	29.4	Silt	0	0	50	40	60	0	0
39	1	medium	1.24	17.1	S gravel	0	0	50	40	55	1	0
39	2	slow	1.22	21.5	S gravel	0	0	45	35	60	0	0
39	3	slow	1.17	29.4	Silt	0	0	50	40	60	0	0

Table C-6. Habitat measurements for each cell in section 6 (low gradient) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.25	11.3	S gravel	0	0	30	25	40	0	0
0	2	slow	1.11	21.9	S gravel	0	0	45	40	50	0	0
0	3	slow	1.26	23.9	S gravel	0	0	40	40	50	0	0
3	1	slow	1.67	10.5	Silt	0	1	45	35	50	1	1
3	2	slow	1.29	23.4	Cobble	1	0	65	60	70	0	0
3	3	slow	1.33	28.7	S gravel	0	1	60	50	70	0	0
6	1	slow	1.29	16.1	S gravel	0	0	65	50	70	1	1
6	2	slow	1.22	23.3	S gravel	1	0	70	70	80	0	0
6	3	slow	1.34	28.7	S gravel	1	0	70	70	75	1	0
9	1	slow	1.22	11	S gravel	0	0	55	55	60	0	0
9	2	slow	1.20	18.9	S gravel	0	0	50	40	55	0	0
9	3	slow	1.23	20.1	S gravel	0	0	35	30	35	0	0
12	1	slow	1.44	10.2	Silt	0	1	40	30	45	0	0
12	2	slow	1.19	18.6	S gravel	0	0	35	35	45	0	0
12	3	slow	1.16	17.5	S gravel	0	0	25	20	25	0	0
15	1	slow	1.50	10	Cobble	6	1	55	40	60	0	0
15	2	slow	1.19	21.1	Boulder	2	1	45	30	55	0	0
15	3	slow	1.20	17.7	S gravel	0	0	25	20	30	0	0
18	1	slow	1.40	11.4	Boulder	5	0	45	0	50	0	0
18	2	slow	1.21	26.3	Boulder	4	0	55	50	70	0	0
18	3	slow	1.20	18.7	S gravel	0	1	25	20	50	0	0
21	1	slow	1.47	17.5	Boulder	3	1	75	75	85	0	0
21	2	slow	1.42	24.3	Boulder	3	0	50	40	85	0	0
21	3	slow	1.51	27.8	Boulder	2	0	50	30	55	0	0
24	1	slow	1.17	12	S gravel	0	0	35	30	35	1	0
24	2	slow	1.00	17.1	S gravel	0	0	30	30	35	0	0
24	3	slow	1.17	19.4	S gravel	0	0	30	25	35	0	0
27	1	slow	1.11	10.2	S gravel	0	1	40	35	40	1	1
27	2	slow	1.17	17.9	S gravel	0	0	35	35	35	0	0
27	3	medium	1.20	24.4	L gravel	1	0	40	30	40	0	0

Table C-7. Habitat measurements for each cell in section 7 (beaver pond) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	velocity	complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.26	18.3	Silt	0	0	50	40	60	0	0
0	3	slow	1.26	18.3	Silt	0	0	50	40	60	0	0
3	1	slow	1.38	13.8	Silt	0	0	45	40	60	0	0
3	3	slow	1.38	13.8	Silt	0	0	45	40	60	1	0
6	1	slow	1.65	18.5	Silt	0	0	65	60	70	0	0
6	3	slow	1.65	18.5	Silt	0	0	65	60	70	0	0
9	1	slow	1.47	15.2	Silt	0	0	45	40	60	0	0
9	3	slow	1.47	15.2	Silt	0	0	45	40	60	0	0
12	1	slow	1.60	15.6	Silt	0	0	50	40	60	0	0
12	3	slow	1.60	15.6	Silt	0	0	50	40	60	0	0
15	1	slow	1.36	13.3	Silt	0	0	35	30	40	0	0
15	3	slow	1.36	13.3	Silt	0	0	35	30	40	0	0
18	1	slow	1.29	13.2	Silt	0	0	35	35	40	0	0
18	3	slow	1.29	13.2	Silt	0	0	35	35	40	0	0

Table C-8. Habitat measurements for each cell in section 8 (beaver pond) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	velocity	complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.86	16.1	Silt	0	0	65	50	70	0	0
0	3	slow	1.86	16.1	Silt	0	0	65	50	70	0	0
3	1	slow	1.13	17.5	Silt	0	0	35	30	35	0	0
3	3	slow	1.13	17.5	Silt	0	0	35	30	35	1	1
6	1	slow	1.30	19.7	Silt	0	0	45	40	45	0	0
6	3	slow	1.30	19.7	Silt	0	0	45	40	45	0	0
9	1	slow	1.52	22.1	Silt	0	0	60	50	85	0	0
9	3	slow	1.52	22.1	Silt	0	0	60	50	85	0	1
12	1	slow	1.60	16.1	Silt	0	0	55	50	65	0	0
12	3	slow	1.60	16.1	Silt	0	0	55	50	65	1	1
15	1	slow	1.28	17	Silt	0	0	45	35	50	0	0
15	3	slow	1.28	17	Silt	0	0	45	35	50	0	0

Table C-9. Habitat measurements for each cell in section 9 (beaver pond) of the 1996 competitor addition and ordering effects experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	velocity	complexity	hydraulic radius	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	1.00	16.3	Silt	0	0	35	20	40	0	0
0	2	slow	1.02	29.3	Silt	0	0	55	55	60	0	0
0	3	slow	1.13	31.5	Silt	0	0	50	45	60	1	0
3	1	slow	1.14	14.5	Silt	0	0	45	15	50	0	0
3	2	slow	1.08	28.6	Silt	0	0	55	50	60	0	0
3	3	slow	1.15	30.9	Silt	0	1	50	40	50	1	0
6	1	slow	1.00	15.8	Silt	0	0	45	40	50	0	0
6	2	slow	1.10	28.6	Silt	0	0	55	55	60	0	0
6	3	slow	1.11	32.9	Silt	0	0	50	40	60	1	1
9	1	slow	1.23	13.8	Silt	0	0	45	35	50	0	0
9	2	slow	1.11	28.2	Silt	3	0	55	50	60	0	0
9	3	slow	1.12	27.4	Silt	0	0	40	35	50	0	0
12	1	slow	1.20	11.4	Silt	0	0	45	45	50	0	1
12	2	slow	1.08	22.5	Silt	0	0	55	55	60	0	0
12	3	slow	1.13	23.7	Silt	0	0	40	35	50	0	1
15	1	slow	1.29	8.4	Silt	0	0	40	35	45	0	0
15	2	slow	1.04	20.6	Silt	0	0	50	45	50	0	0
15	3	slow	1.14	24.7	Silt	0	0	45	40	50	0	0

Table C-10. Habitat measurements for each cell in section 1 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	medium	medium	cobble	2	0	25	0	30	0	0
0	2	medium	high	cobble	1	0	35	10	40	0	0
0	3	medium	high	cobble	4	0	35	0	40	0	0
3	1	slow	low	s gravel	0	1	40	0	55	0	1
3	2	medium	medium	cobble	2	0	40	10	50	0	0
3	3	medium	high	cobble	1	0	35	10	45	1	0
6	1	slow	high	s gravel	0	2	45	10	60	0	1
6	2	medium	medium	boulder	3	1	40	10	65	0	0
6	3	slow	medium	l gravel	2	0	30	10	35	1	0
9	1	slow	high	boulder	1	1	45	10	55	0	1
9	2	medium	medium	s gravel	2	2	50	45	55	0	0
9	3	slow	low	silt	0	1	40	10	50	0	0
12	1	slow	medium	s gravel	2	2	30	20	45	0	1
12	2	medium	low	s gravel	0	2	45	35	65	0	0
12	3	slow	medium	silt	0	3	45	10	60	0	0

Table C-11. Habitat measurements for each cell in section 2 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	medium	silt	0	0	30	30	30	0	0
0	2	slow	medium	silt	0	0	35	35	40	0	0
0	3	slow	medium	silt	0	0	30	30	30	0	0
3	1	slow	high	silt	0	0	25	20	30	1	0
3	2	slow	medium	l gravel	0	0	45	30	60	0	0
3	3	slow	medium	l gravel	0	0	50	40	65	1	0
6	1	slow	medium	silt	0	0	40	25	55	1	0
6	2	slow	medium	l gravel	0	0	65	60	75	0	0
6	3	slow	medium	silt	0	0	35	35	40	1	1
9	1	slow	medium	s gravel	0	0	35	30	40	0	0
9	2	slow	low	cobble	1	0	50	40	65	0	0
9	3	slow	medium	silt	0	0	35	30	35	0	1

Table C-12. Habitat measurements for each cell in section 3 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	low	s gravel	0	0	35	30	40	0	0
0	2	slow	low	boulder	1	0	50	40	60	0	0
0	3	medium	medium	l gravel	1	0	30	25	30	0	1
3	1	slow	medium	s gravel	0	0	40	30	50	0	0
3	2	slow	medium	cobble	3	0	50	25	60	0	0
3	3	slow	medium	boulder	2	0	40	0	55	0	1
6	1	slow	high	s gravel	0	0	50	40	60	1	0
6	2	slow	low	cobble	0	0	60	55	70	0	0
6	3	slow	medium	cobble	1	0	40	20	40	0	0
9	1	slow	low	l gravel	0	0	65	65	65	0	0
9	2	slow	low	boulder	0	0	55	50	65	0	0
9	3	slow	low	silt	0	0	40	30	50	0	0
12	1	slow	high	cobble	1	0	50	40	70	1	1
12	2	slow	medium	l gravel	1	0	65	65	70	0	0
12	3	slow	medium	silt	0	0	40	30	45	0	0

Table C-13. Habitat measurements for each cell in section 4 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	high	s gravel	0	0	30	30	35	0	0
0	2	slow	medium	s gravel	0	0	40	35	40	0	0
0	3	slow	medium	s gravel	0	0	40	35	40	1	0
3	1	slow	medium	s gravel	0	0	35	30	40	0	0
3	2	slow	low	s gravel	0	0	35	30	40	0	0
3	3	slow	medium	s gravel	0	1	40	35	40	1	0
6	1	slow	medium	s gravel	0	0	60	60	65	1	0
6	2	slow	low	s gravel	0	1	60	55	65	0	0
6	3	slow	medium	s gravel	0	1	55	50	60	1	0
9	1	slow	medium	s gravel	0	0	40	40	55	1	0
9	2	slow	low	l gravel	0	0	60	50	70	0	0
9	3	slow	high	s gravel	0	0	60	50	70	1	0

Table C-14. Habitat measurements for each cell in section 5 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	low	s gravel	0	0	30	25	40	0	0
0	2	slow	low	l gravel	0	0	60	50	60	0	0
0	3	slow	low	silt	0	0	45	40	60	1	0
3	1	slow	high	s gravel	0	0	35	25	40	0	0
3	2	slow	high	boulder	2	0	60	55	60	0	0
3	3	slow	high	silt	1	0	25	20	40	0	0
6	1	slow	high	s gravel	0	0	35	30	40	0	0
6	2	slow	medium	cobble	3	0	55	50	60	0	0
6	3	slow	medium	cobble	2	1	30	25	40	0	0
9	1	slow	high	s gravel	0	0	45	30	50	0	0
9	2	slow	medium	cobble	0	0	55	50	60	0	0
9	3	slow	medium	boulder	1	0	40	30	45	0	0

Table C-15. Habitat measurements for each cell in section 6 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	high	s gravel	0	0	55	55	60	0	0
0	2	slow	medium	s gravel	0	0	55	50	65	0	0
0	3	slow	medium	silt	0	1	45	40	60	0	0
3	1	slow	high	s gravel	0	0	55	55	60	0	0
3	2	slow	medium	s gravel	0	0	65	60	65	0	0
3	3	slow	medium	silt	0	0	50	45	60	0	0
6	1	slow	medium	s gravel	0	0	55	50	60	1	0
6	2	slow	low	s gravel	0	0	65	60	70	0	0
6	3	slow	low	silt	0	0	50	40	60	0	0
9	1	medium	medium	s gravel	0	0	50	40	55	1	0
9	2	slow	medium	s gravel	0	0	45	35	60	0	0
9	3	slow	low	silt	0	0	50	40	60	0	0

Table C-16. Habitat measurements for each cell in section 7 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	medium	s gravel	0	0	30	25	40	0	0
0	2	slow	low	s gravel	0	0	45	40	50	0	0
0	3	slow	medium	s gravel	0	0	40	40	50	0	0
3	1	slow	high	silt	0	1	45	35	50	1	1
3	2	slow	medium	cobble	1	0	65	60	70	0	0
3	3	slow	medium	s gravel	0	1	60	50	70	0	0
6	1	slow	medium	s gravel	0	0	65	50	70	1	1
6	2	slow	medium	s gravel	1	0	70	70	80	0	0
6	3	slow	medium	s gravel	1	0	70	70	75	1	0
9	1	slow	medium	s gravel	0	0	55	55	60	0	0
9	2	slow	medium	s gravel	0	0	50	40	55	0	0
9	3	slow	medium	s gravel	0	0	35	30	35	0	0

Table C-17. Habitat measurements for each cell in section 8 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	medium	low	s gravel	0	0	20	0	30	0	1
0	2	medium	medium	s gravel	1	0	35	30	40	0	0
0	3	medium	high	cobble	1	0	30	20	40	0	0
3	1	slow	low	s gravel	1	0	25	15	35	0	1
3	2	medium	high	boulder	4	0	35	20	40	0	0
3	3	fast	high	cobble	3	0	35	20	40	0	0
6	1	slow	low	silt	0	0	30	20	35	0	1
6	2	fast	high	cobble	1	0	30	30	45	0	0
6	3	slow	high	silt	2	0	25	30	20	1	0
9	1	fast	high	cobble	0	1	35	30	40	0	1
9	2	fast	high	l gravel	1	0	30	25	30	0	0
9	3	medium	low	silt	1	0	15	0	25	0	0

Table C-18. Habitat measurements for each cell in section 9 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	low	silt	0	0	20	0	25	0	0
0	2	medium	low	l gravel	0	0	25	20	30	0	0
0	3	medium	low	l gravel	0	0	25	0	25	0	0
3	1	slow	high	cobble	3	0	30	25	30	1	1
3	2	medium	low	l gravel	0	0	30	15	35	0	0
3	3	medium	medium	l gravel	0	0	25	20	30	0	1
6	1	slow	medium	silt	1	0	20	15	20	0	1
6	2	medium	medium	l gravel	0	0	25	25	30	0	0
6	3	medium	low	l gravel	0	0	20	15	25	0	1
9	1	fast	low	s gravel	0	0	5	0	25	1	0
9	2	fast	medium	s gravel	0	0	20	15	25	0	0
9	3	fast	high	l gravel	1	0	20	20	25	1	1

Table C-19. Habitat measurements for each cell in section 10 of the 1997 displacement experiments. Cell 1=left margin, 2=midchannel, 3=right margin.

distance (m)	cell	current velocity	channel complexity	dominant substrate	rocks	LWD	mean depth (cm)	minimum depth (cm)	maximum depth (cm)	undercut banks	overhead cover
0	1	slow	low	silt	0	0	20	0	25	0	0
0	2	medium	low	l gravel	0	0	25	20	30	0	0
0	3	medium	low	l gravel	0	0	25	0	25	0	0
3	1	slow	high	cobble	3	0	30	25	30	1	1
3	2	medium	low	l gravel	0	0	30	15	35	0	0
3	3	medium	medium	l gravel	0	0	25	20	30	0	1
6	1	slow	medium	silt	1	0	20	15	20	0	1
6	2	medium	medium	l gravel	0	0	25	25	30	0	0
6	3	medium	low	l gravel	0	0	20	15	25	0	1
9	1	fast	low	s gravel	0	0	5	0	25	1	0
9	2	fast	medium	s gravel	0	0	20	15	25	0	0
9	3	fast	high	l gravel	1	0	20	20	25	1	1

Appendix D.

Invertebrate Drift Abundance

Table D-1. Number of drifting invertebrates collected in the 1-hour drift samples in each reach habitat type.

	High Gradient	Low Gradient	Beaver Ponds
Dipteran larvae	3420	3984	2352
Dipteran pupae	284	256	200
Ephemeroptera	524	240	372
Trichoptera	256	36	24
Plecoptera	24	36	16
Coleoptera	116	84	12
Terrestrial	592	272	176
Total	5216	4908	3152

Appendix E.

Summary of Fisher's Exact Comparisons

Table E-1. Summary list of probabilities of Fisher's exact comparisons for the ordering effects trials comparing habitat use of residents during the three day acclimation period to habitat use when forced to invade sections. Entries with N/A represent those sections where tests could not be carried out.

Section	Trial 1	Trial 2	Trial 3	Trial 4
1	< 0.001	<0.001	0.031	0.004
2	<0.001	0.35	0.44	N/A
3	<0.001	<0.001	0.359	N/A
4	<0.001	<0.001	0.029	0.001
5	<0.001	<0.001	0.034	<0.001
6	<0.001	N/A	N/A	<0.001
7	N/A	<0.001	<0.001	0.07
8	<0.001	<0.001	<0.001	<0.001
9	0.002	<0.001	0.315	<0.001

Appendix F.

Results of Power Analyses

Table F-1. Results of power analyses

Description of Test	Power
ANCOVA of growth for sedentary and mobile cutthroat trout, Table A-1	0.81
ANCOVA of growth by habitat type for sedentary cutthroat trout, Table A-2	0.47
ANCOVA of growth by habitat type for mobile cutthroat trout, Table A-3	0.13
ANCOVA of growth between brook and cutthroat trout, Table A-4	0.13
ANOVA of drifting invertebrates by habitat type, Table B-1	0.10
ANOVA of effect of species of competitor on threshold density, Table B-2	0.37
ANOVA of effect of habitat type on threshold density, Table B-3	0.06
ANOVA of effect of species of competitor on threshold density for high gradient, Table B-4	0.28
ANOVA of effect of species of competitor on threshold density for low gradient, Table B-5	0.07
ANOVA of effect of species of competitor on threshold density for beaver ponds, Table B-6	0.06

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